# MOTIVATION, CONSTRAINT AND ASSOCIATION: AN ANALYSIS OF KILLEEN'S (1994) MATHEMATICAL PRINCIPLES OF REINFORCEMENT

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**Abstract**

Mathematical principles of reinforcement (MPR; Killeen, 1994) is a useful model for predicting and describing behaviour. MPR is based upon three general principles represented by three independent parameters in the model: (1) incentives elicit responses and the quality or amount of a reinforcer will effect organisms arousal and motivation to work for that particular reinforcer (specific activation; *a* in the model), (2) there are time and energy constraints on responding resulting in ceilings on response rates (constraint; δ), and (3) reinforcement only occurs to the extent that responses are associated with reinforcers (Coupling; c.). This experiment tested the ability of MPR to predict response rates when the minimum force requirement to make a response and the reinforcer duration was increased.

Five hens responded on a geometric fixed ratio (FR) schedule in three conditions; low force requirement, small reinforcer (0.24 N, 2-s access), high force requirement, small reinforcer (1.1 N, 2-s access) and high force requirement, large reinforcer (1.1 N, 4-s access). Response rates were well described by a bitonic function as predicted. Response rates were higher and the hens ceased responding at higher FR values when the force requirement was low. Constraint (δ) was not significantly affected by the increase in force requirement. Interestingly, estimates of *a* were most effected by the increase in force requirement. Estimates of *a* were not affected by the increase in the magnitude of the reinforcer. It was concluded that doubling the incentive value may require more than doubling the amount of reinforcement. Additionally, there may be a need to distinguish between time to make a response and effort required with the latter impacting more on the motivation of the organism.

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## Introduction

Two major research activities of experimental psychologists and behaviour analysts are to describe and predict behaviour. These two activities are closely related. Collections of facts without organised explanations are difficult to evaluate for importance. Additionally, theories without substantial empirical support are difficult to evaluate for accuracy (Church, 1997). Both experimental and applied research have documented the effects that schedules of reinforcement have on behaviour.

Reinforcement can be described as a process by which an incentive (reinforcer) is paired with a behaviour and therefore increases the likelihood of that behaviour occurring. Reinforcement both encourages behaviour and directs it (Killeen & Sitomer, 2003). It encourages behaviour by creating an increased state of arousal, one that can become conditioned to the context in which reinforcement occurs. It directs behaviour by activating those responses that precede and predict the reinforcer (Killeen & Sitomer, 2003). The arousal and the direction of behaviour, as a result of reinforcement, act under the constraint of the time it takes to make a response and the energy available to execute a response (Killeen & Sitomer, 2003). Reinforcement can control aspects of the response along multiple dimensions including topography, context, force, and rate (Killeen, 1994).

Particular schedules of reinforcement determine the responding that is required of the organism in order to receive reinforcers. Schedules of reinforcement can also be described as experimental contingencies, which are the conditions that are set by the experimenter as criteria for reinforcement; they put responding in contact with incentives which in turn, determines behaviour of an organism. Ferster and Skinner (1957) referred to behaviour on a schedule of

reinforcement as operant behaviour. Both the speed and orientation of behaviour are affected by how the incentive is scheduled with respect to the target responses; what Skinner (1938) termed the *contingency of reinforcement*.

Ferster and Skinner (1957) described in detail the different patterns of behaviour produced by different schedules of reinforcement. Depending on the type of schedule in effect, an organism's rate and pattern of responding changes. The most commonly documented schedules of reinforcement include schedules that are fixed or variable and interval or ratio in requirement. When schedules are described as fixed, that means that reinforcement is contingent on a response after some fixed period of time or after a fixed number of responses. When a schedule is described as variable, the availability of reinforcement is variable around some mean duration or mean number of responses. On interval schedules, reinforcement is delivered after a fixed or variable time since the previous reinforcer was received. On a ratio schedule it is delivered after either a fixed or variable number of responses since the previous reinforcer was delivered. There is an extensive volume of literature on schedules of reinforcement and the behavioural patterns elicited by the differing schedules.

Fixed ratio (FR) schedules require a fixed number of responses to obtain a reinforcer (Ferster & Skinner, 1957). Reinforcers are delivered after every $n^{th}$ response since the previous reinforcer was delivered. For example, on an FR (5) schedule, the subject would be required to respond five times and then a reinforcer would be provided. In FR schedules the rate of reinforcement is therefore directly and positively related to the rate of responding; the faster the rate of responding, the greater the rate of reinforcement. FR schedules tend to produce a high rate of responding and are characterised by a pause in responding following reinforcer

delivery. The length of the post-reinforcement pause (PRP) characteristically increases as the FR requirement increases. The increase in the PRP, as the ratio requirement increases, results in the response rates decreasing. Typically, on lower FR values, the rate of responding returns to a high rate following the pause (Ferster & Skinner, 1957). Naturally, as the schedule increases, at the higher FR values there is a decrease in overall response rates, eventually resulting in the organism ceasing to respond altogether (Pear, 1975). Bizo and Killeen (1997), through graphing the run rates (response rates when the length of the PRP is discarded), identified that the decrease in the rate of responding is not solely due to an increase in the PRP length. As noted by Zeiler and Buchman (1979), two counterpoised forces affect the control of behaviour under schedules of reinforcement: as the rate of reinforcement is increased, more behaviour is activated, but at the same time the number of responses that each reinforcer can influence is decreased (Killeen, 1994).

Mathematical models of behaviour allow for a way of describing behavioural patterns on different schedules of reinforcement. Through mathematical modelling it is possible to describe behavioural patterns such as the changes in response rates when the FR value is changed. Behaviour analysts are interested in describing functional relationships between classes of variables and their effects on behaviour in order to account for variations in behaviour (Tsibulsky & Norman, 2007). To be most useful such descriptions should be accurate, concise and applicable to a wide range of particular cases (Shull, 1991). A mathematical description of a data set simplifies the way that behaviour is understood. It connects a basic set of common principles that can be applied and tested in different contexts (Killeen, 1992). It is possible to form a quantitative

model predicting behavioural patterns because of common patterns in responding under different schedules in reinforcement or response-reinforcer contingencies. Equations can be developed by reviewing the distributions of many responses and the mathematical functions these resemble (Shull, 1991).

A quantitative model requires that the behaviour be categorised and measured first (Ferster & Skinner, 1957). In order for an equation to be classified as a model it must be accompanied by a sound set of principles and assumptions that have been found to describe an aspect of behaviour (Church, 1997). Principles are described as the skeleton of a theory while the mathematical models put those principles in contact with the data (Killeen & Sitomer, 2003). It should be noted however, that simply because an equation may fit a data set well it does not necessarily mean that the assumptions that underpin the fitting of model to data are correct (Shull, 1991). Within most models there is room for improvement (Church, 1997). If the process leading to the behaviour is a simple one, this function will also be simple, but functions can also interact, suggesting several processes giving rise to the expressed behaviour may be at work at any given time (Church, 1997). A model can therefore be thought of as a strong metaphor (Killeen, 1992; Killeen & Sitomer, 2003) and in this way can assist understanding of not only the processes it was set up to describe, but also offer insight into other aspects of behaviour. To test the model it is highly desirable to have a large number of observations of behaviour (Ferster & Skinner, 1957).

One quantitative model that aims to describe and predict animal's response rates while responding under different schedules of reinforcement is Mathematical Principles of Reinforcement (MPR; Killeen, 1994). MPR is a general theory of operant behaviour proposed by Killeen (1994) which identifies three principles

underlying control of behaviour by reinforcement; arousal, constraint and association. It generally states that incentives excite behaviour, particularly those that precede and predict it, there are temporal constraints on responding and the coupling in memory of responses and reinforcers strengthen behaviour by creating an associative bond. These principles are represented in the formal quantitative model by different parameters which are the fundamental components of Killeen's MPR model. Each parameter identifies a different causal factor in the control of behaviour; specific activation (*a*), constraint (δ) and the coupling coefficient (*c*.). Equation 1 represents the basic model of MPR that expresses behaviour as a function of reinforcement:

$$B = \frac{c.}{\delta} - \frac{n}{\delta a} \quad (1)$$

Where B represents the response rate, *c.* represents the coupling coefficient (different formulation for different schedules), δ denotes the minimum time to complete a response, *n* refers to the FR value that the organism is responding on and *a* represents the amount of behaviour that is evoked by the incentive under these conditions with the dimensions of responses per reinforcer.

Research shows that organisms become aroused upon the delivery of food and periodic feeding tends to make the animal increasingly motivated to respond. It is as though the excitement itself cumulates and does so increasingly with increasing frequency of reinforcers (Killeen, Hansen & Osborne, 1978). After animals are fed there is an increase in general activity and the level of this activity is used as a measure of arousal (Killeen, 1975). The first principle of arousal

describes how reinforcement encourages and motivates behaviour by creating an increased state of arousal which cumulates with feeding. This arousal (A) is proportional to the rate of reinforcement (r) with the constant of proportionality being the parameter known as *specific activation* (*a*) (Killeen & Sitomer, 2003). The parameter *a* increases as a linear function of the rate of feeding. Specific activation is the fundamental factor of the exponential decay curve of response rates when exposed to multiple presentations of incentives, as it decreases at a rate proportional to its current value (Killeen & Sitomer, 2003)**.** If another reinforcer is delivered during decay of arousal the excitement elicited by the second reinforcer adds to what's left of the first reinforcer creating the cumulating effect. This state of arousal decays overtime.

Both arousal level (A=a*r) and specific activation are hypothetical constructs that refer to the motivational state of an organism. It is assumed that the level of arousal is related to the level of deprivation and the quantity and quality of a reinforcer, for a particular organism, at a particular point in time (Killeen & Sitomer, 2003). It represents the number of responses which are activated or supported by each reinforcer. This duration of activation provides a guide of the effectiveness or the 'incentive value' of the reinforcer. Specific activation indicates that an incentive activates *a* responses per reinforcer (Killeen, 1994).

Although the delivery of an incentive does tend to support responding, specific activation has many other influencing factors, including the duration in which the reinforcer is available (Bizo & Killeen, 1997) the physical size or amount of the reinforcer (Bizo & Killeen, 1997; Reilly, 2003) and the economy on which the animal is responding on; whether it is open or closed (Posadas-Sanchez & Killeen, 1995; Zeiler,1999), all of which also effect the animals levels

of satiation (Killeen, 1995; Posadas-Sanchez & Killeen, 1995). Two additional factors must also be considered in translating arousal level into measured rates of target responding. The first is competition from other responses, both from the same operant class and from competing classes (such as focal search). The other factor is the contingency that selects which operant class, either the target or some other, is strengthened by reinforcement and details the topography of that class (Killeen & Sitomer, 2003).

Response rates may also vary considerably even while the motivational state remains unchanged. The general activity of pigeons was explored during the interval between food deliveries (Killeen, 1975). Neither deprivation levels nor the quality of the reinforcer was manipulated across conditions which would mean, theoretically, specific activation and the rate of reinforcement should remain constant. However, response rates fell well below their theoretical asymptote (where they cease responding in this case) and varied substantially due to the contingencies that either reinforced or punished the target response. This series of experiments, ranging over a number of animal species, several classes of behaviour and a variety of experimental conditions, provided the foundation for a mathematical model of temporal control.

The first principle relates rate of reinforcement to arousal and response rates. However, it was also noted that the average response rates, were not exclusively a function of the rate of reinforcement and arousal (Killeen et al., 1978). While responses may be elicited at a rate defined by the first principle it takes time to perform them. The second principle; constraint, characterises limits of responding, such as the time it takes to emit a response and the energy requirements of responding. Constraint refers to the factors unrelated to specific

activation or arousal (including competition from other responses) which may cause response rates to fall short of the theoretical curve (Killeen & Sitomer, 2003). The constraint parameter, delta (δ), accounts for the differences between the rate at which responses are elicited by a stimuli being presented and the rate at which responses can be emitted by the organism. δ captures the number of seconds it takes to make a response, and thus constitutes the minimum response duration an organism is physically able to produce. In addition to the time it takes to make a response, constraint also relates to the inter-response time (IRT) which is the period between the start of one response to the start of the next response. The IRT comprises two sub-intervals; the actual time it takes to make a response and the time between the end of the response to the beginning of the next response (known as Tau; τ). Constraint also then applies to ceilings on responding or maximum attainable responses in a particular period of time calculated as 1/δ. In summary constraint equates to the fact that response rates are constrained by the time and effort required to emit a response (δ). So while responses may be elicited at a rate proportional to A=a*r, they can only be emitted at a particular rate by the organism and consequently are recorded as seconds per response.

The third principle is known as association or coupling and describes the relationship between a reinforcer and a response class and therefore determines the likelihood of a target response occurring. Coupling tells us how arousal is associated with the target response. The correlation between the organism's memory and the behaviour measured by the experimenter is given by coupling coefficients, which are derived for various schedules and are specific to those schedules (See Killeen & Sitomer, 2003, p.62, for coupling coefficients for different schedules)**.** The coefficients are inserted into the general model of

arousal and temporal constraint to predict response rates under any scheduling arrangement. The coupling coefficient is therefore not constant rather it varies as a function of the schedule type. Both the control and speed of a response are affected by how the incentive is scheduled with respect to the target responses; the contingencies of reinforcement. The coupling coefficient quantitatively evaluates the strength of the association between the response emitted and the reinforcer (Killeen & Sitomer, 2003). The proportion of memory occupied by the target responses, and thus the effectiveness of the reinforcers, is captured by the coupling coefficient. Coupling is therefore the degree to which memory is filled by target responses and is assumed to function by increasing the probability of whatever responses are present in memory at the time of reinforcement (Killeen, 1994; Lattal & Abreu-Rodrigues, 1994; Killeen, 2001).

When a response is performed it has an effect on the memory of a certain strength which tends to decay over time. As the number of prior target responses gets very large, coupling to the target response approaches 1. The strength of the coupling coefficient should not reach a value of 1 as reinforcement does not only act on the response immediately preceding the reinforcer. Reinforcement also acts on any other responses that preceded reinforcer delivery, that are still present in the organism's memory, such as consummatory and post consummatory behaviour (e.g., focal search), and adjunctive or superstitious behaviours (Killeen & Sitomer, 2003).

The memory trace of a response is strengthened when another response from the same class is emitted (Killeen, 1994). During an FR schedule, for example, all target responses must be emitted before reinforcement is delivered. At lower FR values, the effect of a reinforcer does not contact many responses

because responding is interrupted by feeding and other magazine (hopper) activity. As the FR requirement increases, the effect of each reinforcer contacts more responses, and so the response rate is seen to be increasing. However, at the same time the level of arousal decreases. For this reason MPR predicts a resulting *bitonic* pattern of responding described by an inverted U when response rate is plotted as a function of ratio requirement (Killeen, 1994).

Consummatory responses weaken the association between the target response and reinforcer, and thus results in lower response rates at smaller FR values. This is followed by an expected increase in response rates to a particular point and then a decrease. Once the number of responses has saturated memory, responding is governed only by arousal. The arousal is depicted in the downward part of the inverted U (Killeen, 1994). The satiation hypothesis is an alternative hypothesis for the downturn in response rates at lower FR values (Bizo & Killeen, 1997). It states that if, a) organisms are fed faster at a faster rate, and b) pauses resulting from momentary satiation will constitute a larger proportion of their performance than on higher ratios. If true then if the rate of eating during a session was reduced the inverted U shape should be replaced by a linear function. This effect was researched by Killeen and Smith (1984) who found that consumption and post-reinforcement pauses affected the memory of pigeons when trying to recall pervious target responses.

The lower response rates seen in interval schedules, when compared to FR schedules, are because of the coupling factor. In interval schedules the reinforcer is coupled indiscriminately with both the target responses and any other behaviour's that occur during the interval (Killeen, 1994). Reinforcement acts on everything that the organism does that is contained in its memory, which may not

be the target response defined by the experimenter. This means that any other behaviour the animal performs between reinforcers is also reinforced. So target responses in interval schedules are coupled with a lower proportion of the target responses than under ratio schedules (Killeen, 1994).

The coupling coefficient (*c.*) for FR schedules is represented by the free parameters lambda; λ and epsilon; ε. It is a factor of constraint (δ) and the rate at which response traces in memory decay, represented by (λ). The reciprocal of lambda tells us the average number of responses that are therefore coupled to a reinforcer in memory. Epsilon (ε) is the parameter intended to reflect the degree to which the memory of the target response is erased between responses (Killeen & Sitomer, 2003). Equation 2; the coupling coefficient for FR schedules is expressed as:

$$CFRn = 1 - \varepsilon e^{-\lambda\delta N} \tag{2}$$

See Table 1 for mathematical symbols and explanations including units of measurement. Values for ε can vary between 0 and 1, with 1 representing complete erasure, and 0 representing total recall. Thus, taking into consideration the coupling coefficient for FR schedules, the formal quantitative model is expressed in Equation 3:

$$B = \frac{\mathbf{1} - \varepsilon \boldsymbol{e}^{-\lambda\delta \mathrm{N}}}{\delta} - \frac{\boldsymbol{N}}{\delta a} \tag{3}$$

MPR has also proven its utility and effectiveness at predicting response rates on other schedules of reinforcement including interval schedules (Killeen, 1994) variable ratio (VR) schedules (Bizo, Kettle & Killeen, 2001; Bizo, Remington, D'Souza, Heighway & Baston, 2002; Killeen & Sitomer, 2003), and progressive ratio schedules (PR; a progressing number of ratio values in the one session; Covarrubias & Aparicio, 2008; Rickard**,** Body, Zhang, Bradshaw & Szabadi, 2009). The MPR model also provides a good prediction of obtained response rates for different species including humans (Bizo et al.,2002) pigeons ( Bizo & Killeen, 1997; Killeen, 1994) rats (Bizo et al., 2001; Sanabria, Acosta, Killeen, Neisewander & Bizo, 2008; Rickard et al., 2009), hens (Stuart, 2013; Bjarnesen, 2011) and possums (Jenkins, 2014).

The four graphs in Figure 1 illustrate the hypothetical effects on response rates as a result of a change in parameter values, with increasing FR values. The changes in parameters tend to affect both the gradient and the intercept of the plotted lines. It is obvious that there is a typical pattern of responding that is bitonic in nature; response rates increase to a maximum value before decreasing over successively larger values (Bjarnesen, 2011; Bizo et al.. 2001; Killeen, 1994). This can be viewed as counterintuitive as the higher response rates are not at the smaller ratio values.

Table 1.

The Mathematical symbols in MPR, their explanations and units of measurement.

| Symbol | Name | Explanation and Units of Measurement |
|---|---|---|
| *a* | Specific activation; | The number of responses of duration δ that will be supported by a given incentive under particular operative motivational conditions. Measures value of an incentive and motivation of the organism; Number of responses/reinforcer. |
| A | Arousal level | Governs asymptotic response rate when characteristics of the sensor, duration of a response, and competition from other responses are taken into account. |
| δ | Delta; response duration | Minimum time required for a single response cycle; reciprocal of maximum response rate. Made up of two parts; time to make a response and time between responses (tau; τ). Seconds/response. |
| C. | Coupling coefficient | Represents the degree to which target responses and reinforcers are associated in the organism's short term memory. Its expected value depends on the schedule of reinforcement and rate of responding. It is made up of λ and ε in FR schedules. Varies between 0-1. |
| λ | Lambda | Measured rate of decay of short term memory (decay of response traces). Average number responses coupled to a reinforcer in STM. Average number responses /reinforcer |
| ε | Epsilon | Degree to which the memory of target response is erased between responses 0-1; 0=total recall and 1 =no recall. |

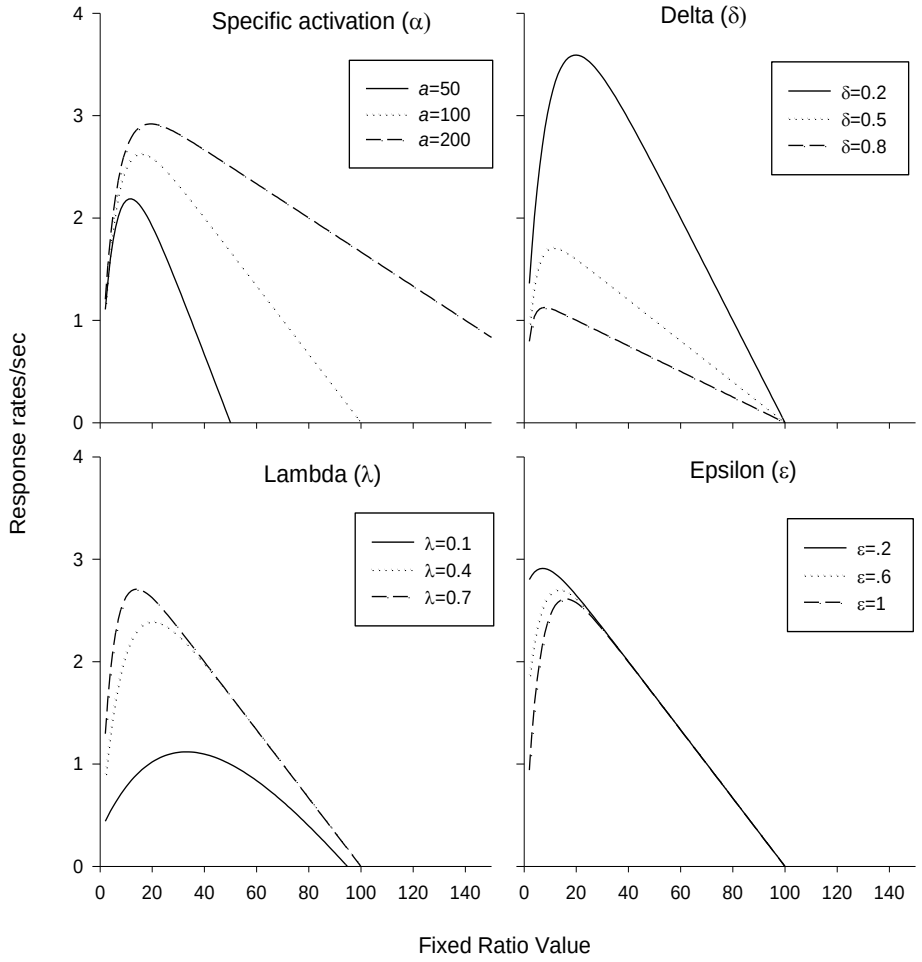


Figure 1. Theoretical FR functions representing the changes in response rates as an effect of change in the values of parameters a, δ, λ and ε in the model. The curves are drawn by Equation 3. The fixed parameters were a = 100, δ = 0.3, λ = 0.6 and ε = 0.9.

The ability of MPR to accurately predict response rates on ratio schedules was tested by Bizo and Killeen (1997) using pigeons responding for known preferred foods. In Experiment 2 specific activation was expected to increase with the level of deprivation and with reinforcer quality (popcorn vs. millet). As predicted estimates of *a* were highest for the most preferred food (popcorn) and lowest for the least preferred food (millet). Results also showed that the different reinforcers had different estimates of *a.* This leading to the suggestion that specific activation is a measure of reinforcer effectiveness sensitive to

manipulation in quality and quantity of a reinforcer, while δ is affected by the response-force requirements (Bizo & Killeen, 1997). Reilly (2003) also demonstrated that estimates of *a* are influenced by the quality of a reinforcer with rats. Again estimates of *a* were higher for the most preferred foods (sucrose) and lower for the least preferred foods (Noyes pellets). While there were intermediate values for *a* in the sucrose/Noyes pellets condition showing the effects of quality on estimates of *a.* These manipulations showed no significant effect of reinforcer quality on constraint and coupling (Bizo & Killeen, 1997; Reilly, 2003). Jenkins (2014) also found that the quality of food had an effect on possums behavior on FR schedules. Foods that were of a higher quality (more preferred) maintained behaviour to larger FR values than foods of a lower quality. The parameter estimates for specific activation also showed a significant difference in value across the foods.

Bizo and Killeen (1997) also manipulated the quantity of the reinforcer by increasing access to the hopper (2.5-s access to 5-s access). The increase in access to a reinforcer equates to a larger reinforcer due to longer durations of eating time. Estimates of *a* were higher for the larger reinforcer (5-s) than for the smaller reinforcer (2.5-s) when responding for the same food. Bizo et al., (2001) manipulated the number of pellets in order to manipulate the quantity of the reinforcer. Rats exhibited, on average, higher response rates for two pellets than for one pellet indicating again higher response rates for larger reinforcers. It was found that larger reinforcers were able to support responding at higher ratio requirements when smaller reinforcers did not (Bizo et al., 2001). In the same set of experiments it was found that smaller reinforcers resulted in higher response rates at the lower response requirements. They termed this effect *the paradoxical*

*incentive effect*. Reilly (2003) also found the same paradoxical incentive effect when changing the quantity of the reinforcer (one or three Noyes pellets). Lower response rates were associated with the larger reinforcer magnitude at the small FR's, generating smaller estimates of λ. At larger FR requirements lower response rates were associated with the smaller reinforcer magnitude (Reilly 2003).

A series of experiments conducted in the domain of behavioral pharmacology found that MPR was able to model the effects of D-amphetamine on operant, food maintained, behavior (Reilly, 2003). Reilly (2003) examined whether MPR can serve as a model to describe the behavioural mechanisms of drug-behaviour interactions. The aim of this study was to investigate how different administered doses of D-amphetamine increased or decreased operant behaviour on FR schedules. Identifying the parameters affected by drugs could suggest the underlying mechanisms by which drugs modulate response rate**.** It was expected that parameter estimates of specific activation would be higher when rats were dosed on D-amphetamine. In general, D-amphetamine dose-dependently decreased response rates. Increases in response rates were observed at the lower doses, especially at smaller FR's. Responding under the smaller FRs was more resistant to the rate-decreasing effects of the larger doses of D-amphetamine. Response rates when compared across the different dosages showed that D-amphetamine significantly increased both δ and λ but had no significant increase in *a* as it was expected (Reilly, 2003). In fact it had the opposite effect as it decreased *a* at the 1.8 and 3.2 mg/kg doses. MPR was able to offer insight into what processes the D-amphetamine was affecting. This translated to motor disruption, increased impulsivity and at higher doses, decreased incentive of value of food.

A further study applied MPR to characterise the effects of a bilateral infusion of 6-OHDA in rats in order to simulate Parkinson's disease (Avila et al., 2009). It was predicted that decrease in operant behaviour would be due to motor deficits and not due to reduced memory capacity or motivation; which translates to an increase in δ but no changes in *a* or λ The results showed that MPR was able to account for the variance in response rates before and after administration of the drug. Behaviour patterns reflected the bitonic pattern with FR values predicted by MPR. Consistent with reported disruptions in motor behaviour induced by the dopaminergic lesions, estimates of δ increased when dopamine was severely depleted. These studies provide support for the use of MPR to model the effects of pharmacological agents on behaviour. They also portray the usefulness of MPR to assist in determining what effect different pharmacological agents may have on behaviour.

There is a limited amount of research involving specifically manipulating the constraint parameter and modeling the results with MPR. The few studies that have manipulated required response force has shown that: (a) the response rates decrease as force requirements increase (Alling & Poling, 1995; Bizo & Killeen, 1997; Bjarnesen, 2011), (b) extinction is more rapid as force requirements increase (Mowrer & jones, 1943), (c) subjects will escape from situations requiring particularly effortful responding (Miller, 1968), and (d) subject prefer lower effort responding to higher effort responding (Miller 1968; Perone & Baron, 1980).

Alling and Poling (1995) found it was possible to alter typical patterns of responding in a systematic way by altering the response requirements. Their first experiment investigated changes in rats responding over a range of FR values and

force requirements. Weights were added to response levers to alter the minimum force requirement to make a response. One lever always required 0.25 N, and the force requirement for the other lever changed between 0.25 N, 0.5 N, 1 N and 2 N. Overall response rates in the varied-force condition at force requirements of 0.5, 1.0 and 2.0 N were lower than those that occurred at the 0.25 N requirements. There were no consistent changes in response rates during the constant force condition. Results concluded that when the force requirement was increased, the mean IRT increased and the response rates decreased. For some of the rats the rate of the decrease in response rates was proportional to the increase in force requirement. Their second experiment investigated whether the effects of the increases in response force depended on where in an FR 15 schedule those increases occurred. Overall response rates were reduced regardless of its location in the FR15. Experiment 3 was conducted to determine whether decreasing the number of responses to produce reinforcement (from FR 15 to 5 to 1) would influence the effects of altering the amount of force required to operate the lever. Again, overall response rates decreased regardless of how many responses were required to gain access to the reinforcer. This shows that rats are sensitive to changes in force requirement of these magnitudes and even over a small range of FR values the differences in force requirement has a noticeable effect.

Bizo and Killeen (1997) specifically looked at response constraint in relation to MPR. In this investigation the topography of responding was also altered, requiring pigeons to either press a key or depress a foot treadle. This was expected to manipulate the parameter of constraint as it took longer to make the response, with the key peck taking on average 0.32-s and the treadle press an average of 1.12-s to complete. This was to provide further evidence that the

parameter δ reflects differences in response duration. Overall it was predicted that the change in topography would increase delta, decrease response rates and lead to cessation of responding at lower FR values for the treadle. As MPR predicts, the longer response duration resulted in lower response rates. The differences in response rates reflected differences in the estimated δ values and were caused in part by longer PRPs for treadle pressing than key pecking. However, the parameter estimates for specific activation were greater for responding on the treadle which was an unexpected result that is inconsistent with MPR (Bizo & Killeen, 1997).

Bjarnesen (2011) also tested the ability for MPR to predict response rates when the minimum force requirement and the topography of response were changed. Increasing the minimum force requirement was expected to increase the value of δ, the parameter related to response constraint. Altering the topography of the response was also expected to alter the δ value, as the different response forms were expected to take different lengths of time to perform. Six hens responded in four different conditions; low force key, low force door, high force key and high force door in an ascending geometric series of FR values. It was shown that hens responded at a faster rate and to higher FR values when responding on the key than on the door, and for both apparatus the hens stopped responding at lower FR values when the weights were added. Unexpectedly, there was no significant change in the δ value across conditions. Interestingly however, the values for specific activation (*a*), meant to represent arousal, were significantly different across conditions. It was suggested that the changes in *a* reflected changes in the animal's motivation to perform the different responses, due to rewarding or aversive properties of the operant response related to the different response forms.

Considering factors such as response, the animal's levels of motivation, duration or force requirement, and association between the responses and reinforcer allows the experimenter to form a better understanding of the relations between variables and the resulting response patterns. These parameters allow the equation to draw a line through data and both predict and post-dict response rates**.** It is possible to simplify phenomena in order to study and quantify them and then test the developed theory in natural settings (Killeen, 1995). This is often necessary as it is difficult to properly control variables in a natural setting; however, in experimental settings it is possible to systematically manipulate individual variables to better understand their influence on behaviour and enable the development of models to predict behaviour patterns**.** It is important to confirm that the parameters the model asserts are related to motivational or physical aspects of the task vary appropriately when the corresponding aspects are manipulated. Particularly when recent research has resulted in inconsistencies where response force, duration and topography have been altered, which are expected to affect estimates of δ, however, estimates of *a* have been significantly effected (Bizo & Killeen, 1997; Bjarnesen, 2011).

It is also important to assess the ability of this model to predict performance when response requirement is manipulated because it will help disambiguate the relative importance of motivational and physical components of a task which combine to determine the expression of behaviour. This research tends to show systematic deviations from the model particularly in regards to correlations between parameters indicating they are not orthogonal but rather they co-vary. Correlations have been identified between the parameters although not expanded on in great detail. Killeen & Bizo (1997) found positive correlations

between δ and lambda; lower values of lambda corresponded to lower values of δ. Correlations between lambda and δ have been observed showing rate of decay in short term memory covaries with the duration of the response (Killeen, 1994). There have also been negative correlations observed between lambda and specific activation (Bjarnesen, 2011). Nevin (2003) suggests that an increased value of *a* may be the mediator of contrast effects.

The aim of the present experiment was to test the ability of MPR to predict responding on an ascending, geometric series of FR values, when the force requirement to make a response was altered. The present experiment provided an opportunity to assess the influence of manipulations that are assumed by the model to only affect just one parameter; δ. The model predicts that by increasing the force of the response requirement to make an effective response then only the parameter estimate of δ would be altered. It was therefore hypothesised that estimates of δ would increase with an increase in force requirement. It was expected that at lower δ values, responding would occur at a higher rate than at high δ values. As the FR requirement was increased, there would be a bitonic pattern of responding shown by a steep increase in response rates up to a point followed by a gradual decline. Based on the model it was expected that *a* would be relatively constant across conditions, increasing with an increase in the reinforcer, while λ may change as the response duration/force increased but the main change in parameter estimates would be seen in δ. This research should be useful in assessing the orthogonality of the parameters and systematic changes.

## Method

### Subjects

The subjects were five domestic Australorp hens (*Gallus gallus domesticus*) that were housed individually in wire cages measuring 420-mm high x 510-mm wide x 500-mm deep with unlimited access to water. The ventilated room which the hens were housed in was lit on a 12 hour light; 12 hour dark cycle (6am – 6pm). Hens were weighed daily and free feeding weight was established over a period of two months. They were maintained at 80±5% of their free feeding weight throughout the experiment by post session feeding of pellets as required. If they were not within weight range they were not exposed to an experimental session that day. Hens were also provided with grit and vitamins on a weekly basis. All hens had previous experimental experience with key pecking. The experiment was approved by the University of Waikato Animal Ethics Committee, protocol number 890 (see Appendix C).

### Apparatus

The apparatus was an experimental chamber (530-mm high x 565-mm wide x 400-mm deep) located in a room with other experimental chambers. The interior of the chamber was painted white with a black mat. A magazine opening (70-mm wide x 105-mm high) was centrally located on the response panel 110-mm from the floor. The response key was located in the same chamber, to the right of the magazine, 380-mm from the floor and 105-mm from the front of the chamber. The response key was approximately 30-mm in diameter, was made of frosted transparent Perspex and was backlit with a white light**.** Once the hen was placed in the chamber there was a blackout period before the program started and the key was illuminated. If a reinforcer was due, the operandum light was turned off, the magazine light illuminated and the magazine raised in order to provide

access to the reinforcer. The force requirement to activate the response key in the first condition was on average 0.24N. In condition two a weight was added onto the back of the key which resulted in an increase in the force requirement required to an average of 1.1N. Successful responses resulted in an audible beep of 55 dB. The force requirement was tested on a weekly basis. A response was recorded as such if the key peck resulted in a micro switch being opened (the key lifted). The key was required to return to resting position before another response could be performed. When the FR schedule requirement was met, a light above the magazine was illuminated to signify activation of the magazine. The magazine was raised to allow 2-s timed access to wheat. If a hen did not attempt to eat from the hopper within 3-s of the hopper being raised, reinforcer delivery was terminated and the next trial proceeded with the reinforcer recorded as 'non-eat reinforcer'. This occurred only occasionally. The experimental trials and conditions were programmed, recorded and controlled by a PC computer connected to a purpose built interface unit controlled by Delphi software.

**Procedure**

The hens had previously been trained to peck response keys for food reinforcers. Key pecks were reinforced according on a geometric sequence of FR values. The hens were exposed to three sessions on one FR value before progressing to the next FR value. The ratio requirements were 2, 4, 8, 16, 32, 64, 128, 256 and 512. Each session ended when the hen received either 30 reinforcers or after 40-minuntes of key time; time that the key was illuminated and it was possible to make a response. Response rates were calculated over blocks of three sessions by summing the total responses over the three sessions and dividing this by the total runtimes over the three sessions. This was the data that was graphed and modelled. Equation 3 was fitted to the response rates data of the individual

hens in Excel. The parameters across conditions were compared by independent t-tests and correlations between the parameters were also assessed. If the hen received no reinforcers in two consecutive days the series was finished and that FR value was recorded as the breaking point. In Condition 2 a weight of 43.6g was added onto the back of the key resulting in an increase in the force requirement of a successful response to approximately 1.1N. In Condition 3 the weight remained and the access to the magazine increased to 4-s. The same procedure as Condition 1 was used. Experimental sessions were scheduled for seven days a week. Hens were excluded from experimental sessions when their weight was outside the specified weight range consequently they, progressed between schedule requirements at different times. See Table 2 for the number of sessions experienced by each hen in each condition. They could not progress to the next Condition until all hens had completed the previous one.

A first condition using a modified key at a 45 degree angle from the ground, which was thought to emit more natural pecking responses, proved to be unsuccessful. Details of this experiment, such as differences in methodology and the variability in response rates, can be found in Appendix A.

## Results

This experiment exposed five hens to three conditions, a low and high response force requirement; 0.24 N and 1.1 N, with a small reinforcer; 2-s access to food and the high response force requirement with a larger reinforcer amount; 1.1N with 4-s access to food. The response required was a key peck and weights were added to the key to increase the force requirement. The hens' responding was reinforced according to a geometrically ascending series of FR values starting from FR 2 to FR 512. Each condition was repeated once. Hens responded on the same FR value for a minimum of three days (see Table 2 for total number of days on each condition)**.** Mean overall response rates were calculated by dividing the total number of responses over the three sessions by the total key time over the three sessions.

Table 2.

The number of sessions experienced by each hen in each condition

| Hen | Condition 1 | Condition 2 | Condition 3 |
|---|---|---|---|
| 6.1 | 32 | 32 | 32 |
| 6.2 | 34 | 24 | 24 |
| 6.3 | 33 | 20 | 21 |
| 6.4 | 32 | 35 | 24 |
| 6.5 | 35 | 31 | 19 |

Response rates for each hen for the low force and high force, small reinforcer conditions are shown in Figure 2 and for high force, small reinforcer and large reinforcer conditions are shown in Figure 3. The smooth curves through the data represent the best fits of the predictions of MPR to response rates, using

non-linear least squares regression. A semi-log graph plot was used as it is a useful way of visualising data that are related according to an exponential relationship. This kind of plot was useful in this instance as the FR values being plotted covered a large range of values, and the response rates had a restricted range. The semi-log graph displays features in the data that would not easily have been seen if both variables had been plotted linearly (For linear representations of the data see Appendix B).

In all conditions response rates showed a bitonic pattern, where they increased with ratio value up at a point (either FR 16 or 32) and then gradually decreased at the higher FR values. When comparing the response rates in the low and high force requirement conditions with the small reinforcer (Figure 2) it can be seen that hen's response rates typically decreased when the force requirement was increased. This was the case for all but one hen, Hen 6.3, whose response rate was highest at FR 8 (log 0.90) in the high force requirement condition, although the break point (point where a hen ceased responding) was low at FR32. Hens generally ceased responding at lower FR values when the force requirement was increased. All hens ceased responding at FR 512 in the low force condition while they stopped responding at lower FR values in the high force condition with Hens 6.1, 6.2, 6.3, 6.4 and 6.5 ceasing to respond at FR 512, 64, 32, 128 and 256 respectively (see Table 3 for the break points for each hen in each condition).

As seen in Figure 3, although the bitonic pattern of responding is evident, there were no other consistent patterns of responding for all five hens when the reinforcer was increased. The response rates at each FR for the high force, small reinforcer condition; Condition 2 were generally a little higher with the exception of rates at FR 16 and FR 32. Hen 6.1 showed similar patterns of responding in the

high force, small reinforcer (Condition 2) and high force, large reinforcer (Condition 3) conditions. The breaking point was the same at FR 512 and the response rates in both conditions were also similar. Hens 6.2 and 6.3 had a lower breaking point in the high force, small reinforcer condition. However, the response rates were higher in Condition 2 than the large reinforcer condition for both hens. Hen 6.4 had the same breaking point in both conditions and again the response rates were lower in the larger reinforcer condition; Condition 3. While Hen 6.5 was opposite and ceased responding at a lower FR value in the larger reinforcer condition, although the response rates were higher in the large reinforcer condition than in the small reinforcer condition.

Table 3

The break points for each hen in each condition.

| Hen | Condition 1 | Condition 2 | Condition 3 |
|---|---|---|---|
| 6.1 | 512 | 512 | 512 |
| 6.2 | 512 | 64 | 256 |
| 6.3 | 512 | 32 | 64 |
| 6.4 | 512 | 128 | 128 |
| 6.5 | 512 | 256 | 64 |

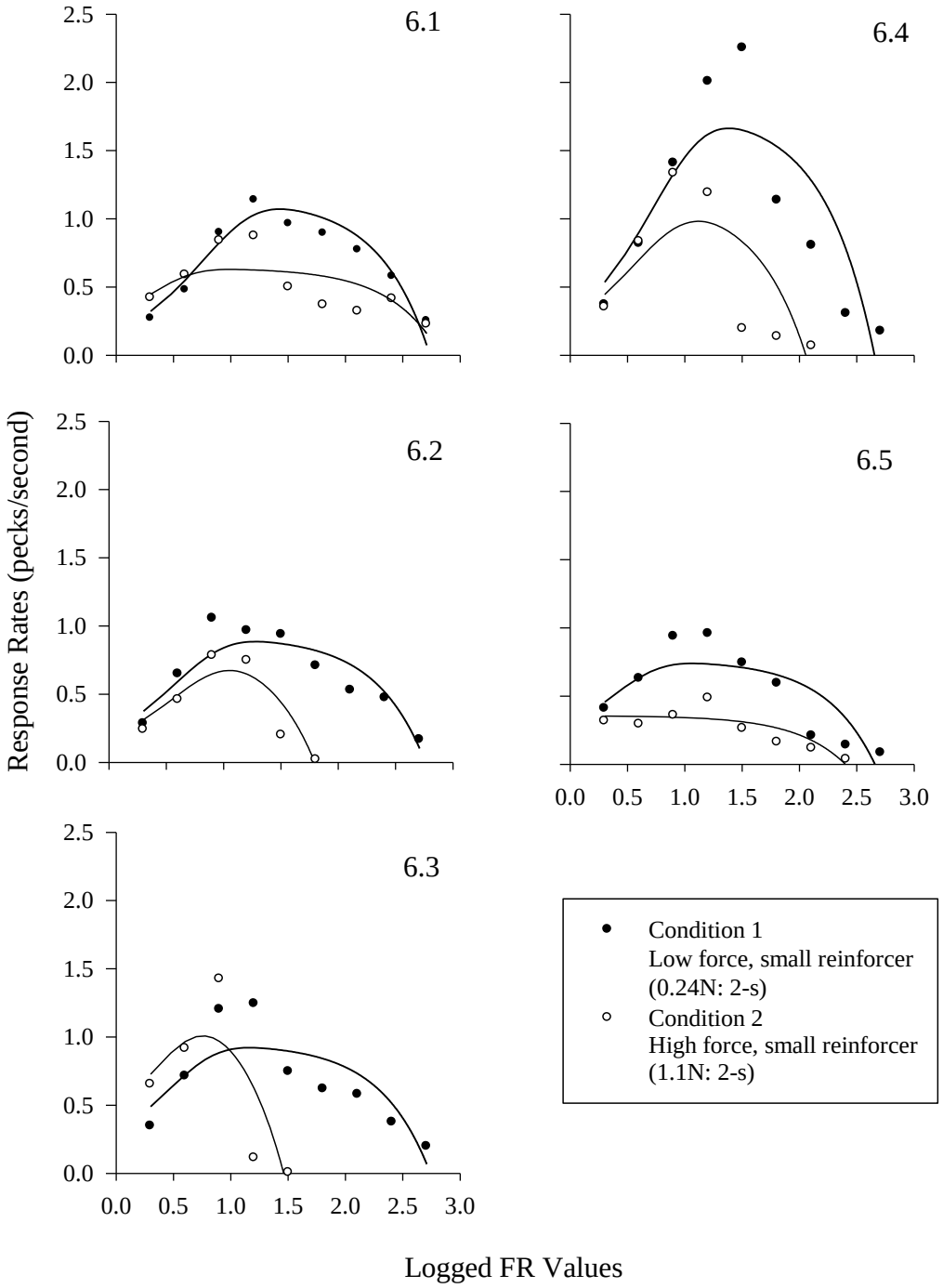


*Figure 2.* Each individual hen's response rates are plotted as a function of logged FR values. These values are calculated by adding the total number of key pecks and dividing this by the total key time for the last three sessions. The lines show the values predicted by equation 3. The filled circles show actual response rates for Condition 1; low force requirement, small reinforcer duration (0.24 N: 2-s) and the unfilled circles represent the actual response rates for Condition 2; High force requirement, small reinforcer duration (1.1 N: 2-s).

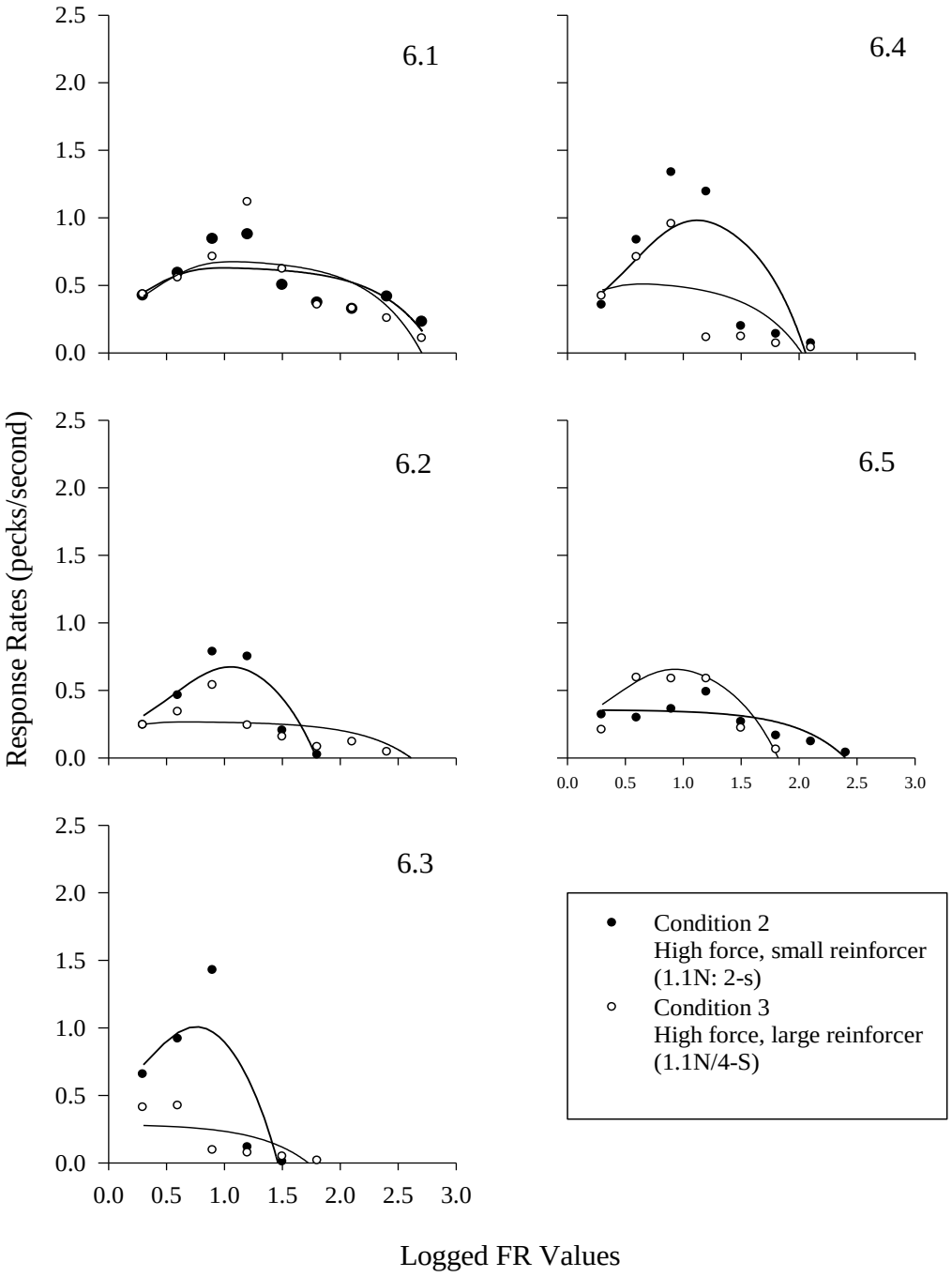


*Figure 3*. Each individual hen's response rates are plotted as a function of logged FR values. These values are calculated by adding the total number of key pecks and dividing this by the total key time for the last three sessions. The lines show the values predicted by equation 3. The filled circles show actual response rates for Condition 2; high force requirement, small reinforcer duration (1.1 N: 2-s) and the unfilled circles represent the actual response rates for Condition 3; High force requirement and large reinforcer duration (1.1 N: 4-s).

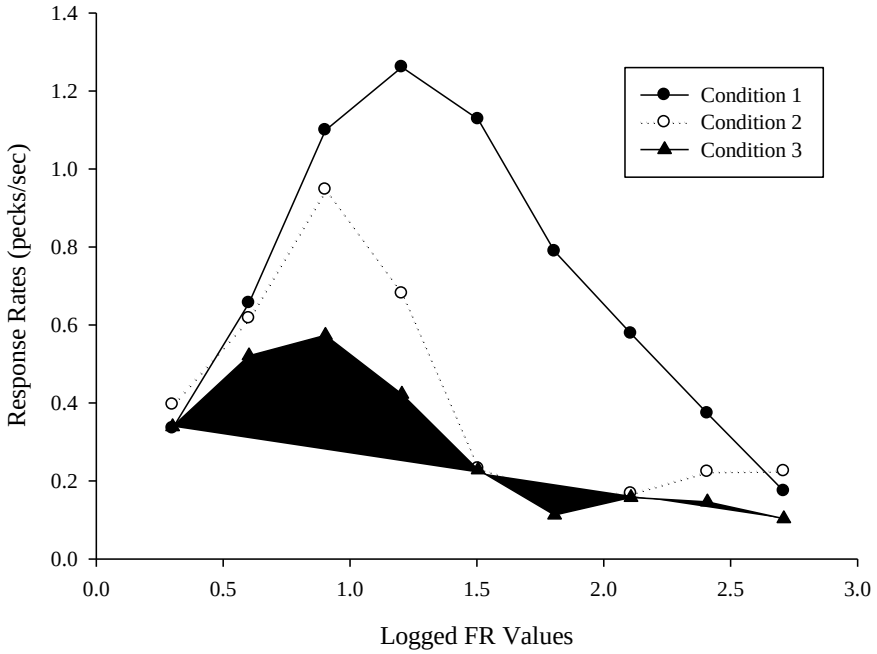


*Figure 4.* Average response rates for logged FR values for all hens over all conditions.

In summary, as the ratio value increased the response rates increased up to a point. All response rates peaked at either FR 16 or 32 before there was a steady decline in response rates at the larger FR values. This bitonic pattern of responding was consistent for all the hens in each condition. There was a general decrease in response rates and earlier break points in Condition 2 when the force requirement to make a response was increased. However, there was no consistent change in response rates or break points when the reinforcer amount was increased. Average response rates for all hens were higher overall in the low force, small reinforcer condition and lowest in the high force, large reinforcer condition (see Figure 4; for a linear representation see Figure 8 in appendix B)

Parameter estimates of *a*, λ, δ and ε were obtained from the best fit of Equation 3 to each individual hen, for each condition. The variation in the FR values at which the hens stopped responding for each condition is captured by the models estimated values for *a*. Manipulating the force requirement was intended to effect delta; δ, the parameter that refers to constraints on responding. These values for each hen across each condition as well as the parameter estimates for lambda; λ and epsilon; ε, including the $R^2$ and the standard error values are compared in Table 4.

Table 5 shows a summary of these values showing the mean, median, range and standard deviation (SD) over all sessions, for all hens, in each condition. Parameter estimates for *a* ranged from 451.2 to 576.3 *(M*=516.2, *SD*=58.7), 29 to 681.5 (*M*=227.6, *SD* 267.6) and 53 to 504.7 (*M*= 227.5, *SD* 212.6) in C*onditions 1, 2 and 3 respectively. Parameter estimates for* λ (which refers to the rate of decay of response traces) are 0.19 to 0.35 (*M*=0.29, *SD*=0.07) in Condition 1, 0.22 to 1.51 (*M*=0.62, *SD*=0.53) in Condition 2 and in Condition 3; 0.30-2.3 *(M*=0.78, *SD*=0.86). Parameter estimates of δ were 0.56-1.31 (*M*=0.98, *SD*=0.28), 0.72-2.80 (*M*=1.41, *SD*=0.84) and 1.27-3.71 (*M*=2.35, *SD* 1.15) for Conditions 1, 2 and 3, respectively. $R^2$ ranged from 0.66-0.89 (*M*=0.75, *SD*=10) with a standard error of the mean of 0.14-0.51 (*M*=0.26, *SD*= 0.15) in Condition 1. The $R^2$ values in Condition 2 ranged between 0.48 and 0.81 (*M*=0.62, *SD*=0.13) with a standard error of the mean of 0.11-0.71 (*M*=0.35, *SD*= 0.25). $R^2$ in Condition 3 were 0.40-0.72 (*M*=0.52, *SD* 0.13) with a standard error of the mean of 0.17-0.40 (*M*=0.25, *SD*, 0.01).

Table 4

*The estimated values of a, λ, δ and ε along with $R^2$ for each fit of Equation 3 to response rates for each hen over all conditions.*

| Hen | Condition | *a* | λ | δ | ε | $R^2$ |
|---|---|---|---|---|---|---|
| 6.1 | 1 (0.24N/2s) | 547.0 | 0.192 | 0.878 | 1 | 0.885 |
| 6.1 | 2 (1.1N/2s) | 681.5 | 0.387 | 1.513 | 1 | 0.479 |
| 6.1 | 3 (1.1N/4s) | 504.7 | 0.324 | 1.44 | 1 | 0.548 |
| 6.2 | 1 (0.24N/2s) | 576.3 | 0.243 | 1.085 | 1 | 0.813 |
| 6.2 | 2 (1.1N/2s) | 62.3 | 0.215 | 1.115 | 1 | 0.809 |
| 6.2 | 3 (1.1N/4s) | 408.1 | 0.36 | 3.71 | 0.99 | 0.457 |
| 6.3 | 1 (0.24N/2s) | 551.4 | 0.347 | 1.051 | 1 | 0.662 |
| 6.3 | 2 (1.1N/2s) | 29.0 | 0.622 | 0.719 | 1 | 0.637 |
| 6.3 | 3 (1.1N/4s) | 53.0 | 2.308 | 3.462 | 1 | 0.478 |
| 6.4 | 1 (0.24N/2s) | 451.2 | 0.324 | 0.562 | 1 | 0.700 |
| 6.4 | 2 (1.1N/2s) | 113.6 | 0.297 | 0.866 | 1 | 0.506 |
| 6.4 | 3 (1.1N/4s) | 105.7 | 0.579 | 1.861 | 1 | 0.392 |
| 6.5 | 1 (0.24N/2s) | 455.0 | 0.352 | 1.311 | 1 | 0.676 |
| 6.5 | 2 (1.1N/2s) | 251.7 | 1.513 | 2.804 | 1 | 0.680 |
| 6.5 | 3(1.1N/4s) | 66.0 | 0.299 | 1.266 | 1 | 0.721 |

Table 5

Minimum, maximum, mean and median values with standard deviations (SD) of estimates for of a, λ, δ, $R^2$ and standard error values, for each hen, over all conditions.

| Condition | Parameter | Minimum | Maximum | Mean | Median | S D |
|---|---|---|---|---|---|---|
| 1 | *a* | 451.2 | 576.3 | 516.2 | 547 | 58.7 |
| (0.24N/2s) | λ | 0.19 | 0.35 | 0.29 | 0.32 | 0.07 |
| | δ | 0.56 | 1.31 | 0.98 | 1.05 | 0.28 |
| | $R^2$ | 0.66 | 0.89 | 0.75 | 0.70 | 0.10 |
| | SE of mean | 0.14 | 0.51 | 0.26 | 0.24 | 0.15 |
| 2 | *a* | 29.0 | 681.5 | 227.6 | 113.6 | 267.6 |
| (1.1N/2s) | λ | 0.22 | 1.51 | 0.62 | 0.39 | 0.53 |
| | δ | 0.72 | 2.80 | 1.41 | 1.12 | 0.84 |
| | $R^2$ | 0.48 | 0.81 | 0.62 | 0.64 | 0.13 |
| | SE of mean | 0.11 | 0.71 | 0.35 | 0.21 | 0.25 |
| 3 | *a* | 53.0 | 504.7 | 227.5 | 105.7 | 212.6 |
| (1.1N/4s) | λ | 0.30 | 2.30 | 0.78 | 0.36 | 0.86 |
| | δ | 1.27 | 3.71 | 2.35 | 1.86 | 1.15 |
| | $R^2$ | 0.40 | 0.72 | 0.52 | 0.48 | 0.13 |
| | SE of mean | 0.17 | 0.40 | 0.25 | 0.21 | 0.01 |

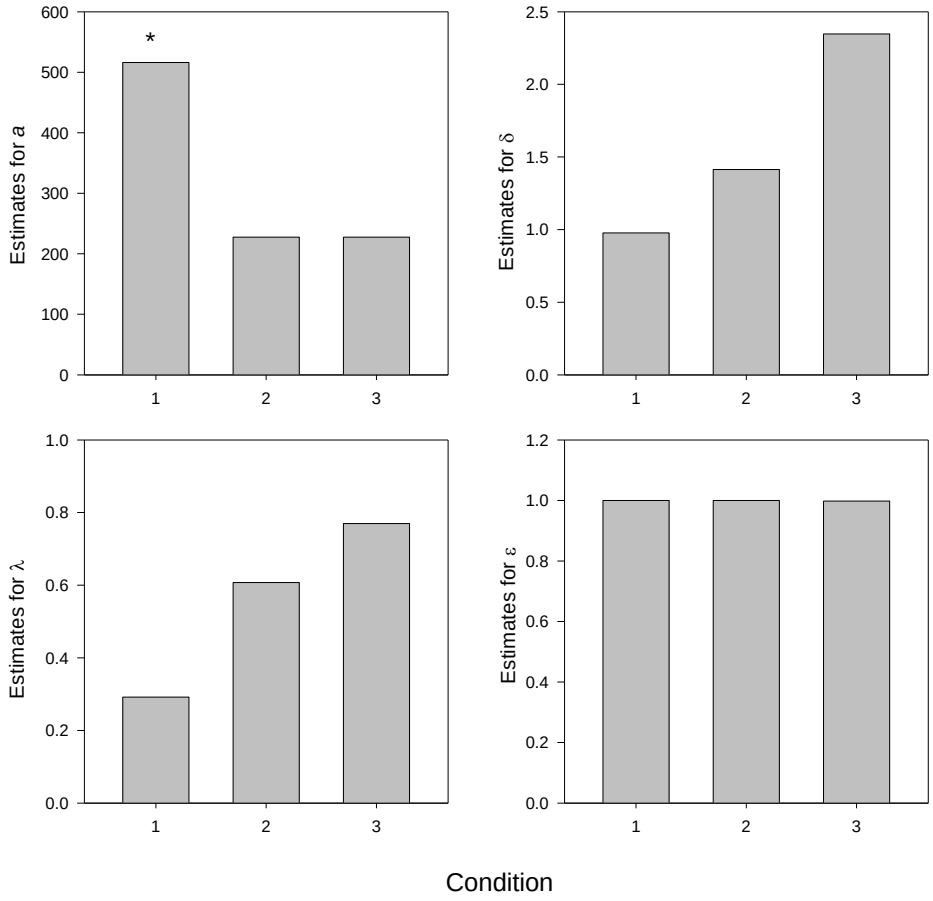


*Figure 5*. Average parameter estimates of all hens for specific activation (*a*), constraint (δ), lambda (λ) and epsilon (ε) in each condition.

As seen in Figure 5, in Condition 1 average estimates for *a* were 516.2 which dropped to 227.6 when the force requirement was increased. The estimates of *a* did not increase with the larger reinforcer in Condition 3, see the top left panel of Figure 4.There was a positive correlation between λ and δ. The estimates for λ showed an increase over conditions starting from 0.29 in Condition 1 and increasing to 0.61 in Condition 2 and 0.77 in Condition 3. δ increased from 0.98 in Condition 1 to 1.41 in condition 2 and 2.35 in Condition 3. The parameters for ε did not change over conditions. See Table 7 for the results of repeated measured dependent t-tests comparing average parameter values across conditions. It was

revealed that parameter *a* (specific activation) was significant between Conditions 1 and 2 t(4)= *2.1,* p=0.04<0.05 and between Conditions 1 and 3 with t(4)= *2.13, p=0.01<005.* See

Table 6

Repeated measured dependant t-tests comparing average parameter values across conditions.

| Condition | *a* | λ | δ |
|---|---|---|---|
| 1 and 2 | t(4)=2.13, p=0.04<0.05 | t(4)=2.13, p=0.11>0.05 | t(4)=2.13, p=0.12>0.05 |
| 1 and 3 | t(4)=2.13, p=0.01<0.05 | t(4)=2.13, p=0.13>0.05 | t(4)=2.13, p=0.31>0.05 |
| 2 and 3 | t(4)=2.13, p=0.37>0.05 | t(4)=2.13, p=0.37>0.05 | t(4)=2.13, p=0.16>0.05 |

## Discussion

This experiment investigated the ability of MPR to predict response rates when force requirement to make a response and duration of the reinforcer was altered. The data predicted using MPR was compared to the actual data obtained. Hen's responded on an ascending, geometric series of FR values that required either 0.24 N or 1.1 N of force and they received either 2-s or 4-s of access to food. In all conditions there was the expected bitonic pattern of responding as predicted by the model, shown by an increase in response rates to a point followed by a decrease. Response rates were higher when force requirement was lower. The hen's ceased responding at lower FR values when the force requirement was increased. In Condition 3, when the reinforce duration was increased to 4-s, at the higher force requirement, there were no consistent effects, on both response rates and break points.

Another aim of the present study was to assess the orthogonality of parameters contained within the MPR model. In MPR these parameters are assumed to be relatively independent. This study aimed to assess how a change in one parameter may, or may not, impact on other parameter estimate values. The increase of force requirement was expected to increase estimates of the constraint; $\delta$ parameter and the increase in access to food was expected to increase estimates of the specific activation; *a* parameter. The increase in force, however, did not significantly affect the constraint parameter although there was an increase of the average parameter values across conditions. Unexpectedly, the estimate value of the specific activation parameter; *a* was significantly higher in the low force requirement condition while paradoxically, it remained unchanged with the larger reinforcer. In summary, while the increase in force requirement had an effect on

response rates and break points it did not have an effect on constraint as predicted but rather, significant changes in *a* were observed.

All the research on MPR and FR schedules has resulted in a bitonic pattern of responding across FR values including previous studies with hen's (Bjarnesen, 2011; Stuart, 2013**)**.The higher response rates and higher break points when there is a low force requirement is consistent with the limited research looking at specifically altering the force requirement of a response. Alling and Poling (1995) indicated that increasing the amount of force required to make a response decreased the rate of responding, increased the PRP and increased all IRTs in the ratio. These results are in agreement with those obtained by previous investigators (Adair & Wright, 1976; Chung 1965; Mower & Jones, 1943; Skinner, 1950), who found that increasing response force reduced response rates. Bjarnesen (2011) and Bizo and Killeen (1997) also reported that response rates and break points were highest for the low force requirement key and lowest for the high force response requirement, regardless of operandum. For two of the hens the larger reinforcers were able to support responding at higher ratio requirements when smaller reinforcers did not (Bizo et al., 2001). Two hens responded to the same FR values with the smaller and larger reinforcer while one hen ceased responding earlier in the larger reinforcer condition. Lower response rates were also associated with the larger reinforcer magnitude particularly at the small FR's. The length of the PRP characteristically increased as the FR requirement increased.

Research investigating the accuracy of predictions of MPR, on FR and other common schedules, has provided mixed findings. The variance accounted for, represented by $R^2$, was used in this study to assess the fits between model and data. $R^2$ is viewed as a conservative index of goodness of fit, as it appropriately

penalises a model for its free parameters (Bizo & Killeen, 1997). The variance accounted for by MPR in this experiment varied between 0.39 to 0.86 which is similar to that found in other research using MPR, FR schedules and hens which ranged from 0.20 to 1.00 (Bjarnesen, 2011) and 0.55 to 0.96 (Stuart, 2013). Covarrubias and Aparicio's (2008) fits with rats responding on PR schedules also had poor and varied fits ranging from 0.03 to 0.90. These fits tend to show worse fits to the data than other papers investigating MPR where $R^2$ is generally less wide-ranging and greater; meaning it is statistically stronger. The mean values of $R^2$ generated by rats responding ranged from 0.886 on a PR schedule (Rickard et al., 2009) to 0.99 on an FR schedule (Reilly, 2003), fits to data generated by pigeons responding on FR schedules ranged from 0.77 to 0.99 (Bizo & Killeen 1997), the $R^2$ values for possums on FR schedules ranged from 0.263 to 0.987 (Jenkins, 2014) and fitting MPR to response rates produced by humans responding on VR schedules resulted in mean $R^2$ values of 0.79 to 0.98 (Bizo et al., 2002).

The poorer fits found in this experiment are similar to other fits generated by hens'. In both Bjarnesen (2011) and Stuart (2013) the fits were calculated after only one session on each FR value. In the present experiment hen's response rates were averaged over three sessions on the same FR value. This is consistent with how the data was analysed in other experiments on MPR using FR schedules that found greater variance accounted for (Bizo et al., 2002; Reilly, 2003 ). However, this did not make a difference. It may be possible that the poorer fits are in part due to variations in species. Bizo and Killeen (1997) looked at how important it is to provide an individual with multiple sessions of experience on each FR requirement and concluded that the number of sessions of exposure to an FR did

not greatly affect response rates. They also concluded that there was insufficient information gained from multiple exposures to each FR value. The results were not tidier with added sessions and therefore the additional resources needed, particularly time, are not justifiable. It therefore, may have been unnecessary to keep them on the same ratio value for three days.

Explanations for poor fits may be assessed by investigating differences between the obtained and predicted response rate values; the residuals. Bjarnesen (2011) found that the residual deviations revealed systematic differences between the obtained and predicted response rate values. MPR tended to underestimate response rates at the low and high FR values and overestimate response rates for the mid-range FR values. If the deviations appeared to be random then those deviations may be attributed to the effect of uncontrolled variables, however, the present study also found the same systematic deviations. Although the magnitudes of the residuals varied between conditions they followed the same pattern as the FR requirement increased, regardless of condition. It is necessary to be careful when interpreting these as all the hens ceased responding at different FR values resulting in more data points at the lower FR values with only a few at the higher FR values. These systematic deviations do however, suggest a weakness in the model, in that it is failing to describe a particular aspect of behaviour (Shull, 1991). Considering the parameter values and the results of an independent t-test between conditions may assist in seeing where this weakness may lie.

MPR is derived from basic principles of reinforcement which are based on the analysis of a large database. Equation 3, which was used to fit the model to the obtained data, consists of four main free parameters $a$, $\delta$, $\lambda$ and $\varepsilon$. These reflect the amount of responding elicited by an incentive of a particular quality and quantity,

under a particular level of deprivation (*a*), the minimum time required to complete a response (δ), the degree of coupling between the reinforcer and the response immediately preceding it (λ) and the degree to which the memory of target response is erased between responses (ε). Surprises in the parameter estimates of the present study, Bizo and Killeen (1997) and Bjarnesen (2011) were not so much related to the adequacy of the quantitative fits between model and data but rather in the interpretation of the parameters.

By altering the variables that contribute to particular parameter values it was expected to see specific changes in the corresponding parameters. Implicit in the constraint parameter is both time to make a response and the effort required. Killeen (1994) suggested that there may be an interaction between the minimum response force and the minimum response duration and therefore incorporated both of these factors into the parameter δ. The change in force requirement when weights were added to the key was expected to increase estimates of δ. Specifically, by increasing the force requirement and therefore making the task more difficult, it was expected the constraint parameter value would increase leading to lower response rates and break points. On average δ did increase across conditions with values lowest in the low force, small reinforcer condition and highest in the high force, large reinforcer condition. The response rates and break points did decrease however; the constraint parameter did not significantly alter between conditions. This is similar to Bjarnesen (2011) when the change in operandum and the different minimum force requirements were also expected to change the estimates for δ. δ was expected to increase from key to door and when weights were added to both however, this also did not occur. Again the response

rates and the break points decreased but the δ parameter did not significantly change.

Response duration enters MPR in two ways. According to the first principle, it affects the number of responses that can be elicited by an incentive and according to the second principle; it determines the ceiling on response rates (Bizo & Killeen, 1997). In MPR both effects were represented by δ. It is obvious that a response that takes a particular time to perform cannot possibly be emitted any faster than 1/ (δ-s) therefore the role of constraint in determining the ceiling rates is secure. However, the effort required to make the response is less clear. Response duration does not always appear to capture the energetic requirements of a response. Killeen (1994) anticipated this possibility, but opted to represent both temporal constraints and energetic requirements as δ, as this proved to be sufficient for the data under his review. Clearly, however, there are cases in which separate representation of the time to complete a response and the effort required is necessary. Bizo and Killeen, (1997) who investigated response requirement in relation to MPR found that the response duration was a poor indicator of the effort expended in forming a response. It was suggested that effort required to complete a response may need to be represented separately from the time to complete a response. As illustrated in the present paper as well as Bjarnesen (2011) and Bizo & Killeen, (1997) it may be important to differentiate between the two factors for a more inclusive representation of response duration and force requirement.

The present experiment specifically aimed to increase the constraint parameter by increasing the force requirement, keeping other factors constant (quality and quantity). The fact that the increase in force did not actually change the parameter it was intended to, in this experiment and similar studies, provide

justification that it may be necessary to differentiate between the two components implicit in δ; time and force. However, the model cannot realistically allocate the different contributions of influencing variables including force requirement, strength, physiological capacity, or refractory period to how fast a response can be repeated, as it would start to have many more parameters if we unravelled them. For reasons of parsimony it is simpler to assert that under constant conditions a certain response will have a minimum response time. Bjarnesen (2011) suggested it is unnecessary to discriminate between the two concepts as the differences in δ values did not alter in a significant manner for both the door and the key when weights were added. This paper went on to state that the only explanation for this that would require a separate parameter would be if the minimum force requirement increased and the hens were able to complete responses faster, cancelling the effect of the force. Although this may help in explaining the effect of no change in the δ parameter, it does not explain the results in regards to the specific activation parameter *a.* This is considered to be a measurement of arousal, motivation or incentive strength. This sensitivity of force requirement equating in a change in *a* may further contribute to the need to differentiate between the time it takes to make a response and the force requirement.

Specific activation; *a* is the number of responses elicited by an incentive. Its value depends on the value of the incentive and the deprivation of the organism. It is predicted to increase with the level of deprivation and with reinforcer quality and quantity. The hens in this experiment were maintained at 85% of their free feeding weight and only participated in experimental sessions when their weight was within 5% of this target. The reinforcer magnitude remained constant between Conditions 1 and 2 and increased between Conditions 2 and 3. These two

aspects meant that theoretically the specific activation parameter *a* should not have varied much between Conditions 1 and 2, but would increase with the larger reinforcer in Condition3. This experiment produced two unanticipated effects on the *a* parameter that were inconsistent with MPR. Firstly, there was a significant increase in the specific activation parameter *a* between Conditions 1 and 2 and Conditions 1 and 3, when there was an increase in force requirement. Secondly, when the duration of the reinforcer was increased between Conditions 2 and 3 estimates of *a* unexpectedly did not increase. These results are consistent with both Bjarnesen (2011) and Bizo and Killeen (1997) who found the same changes in estimates of *a* when manipulating force requirement to make a response.

The larger reinforcer had no consistent effect on response rates. There are some mixed results on the effect of an increase in the amount of a reinforcer. While much research shows it does have an effect on behaviour (e.g. Bizo & Killeen, 1997; Grant et al. 2014) there is also experimental data that show that behaviour is often insensitive to manipulations in the amount of a reinforcer (e.g., Neuringer, 1967), although these experiments generally used interval schedules. These results suggest that the changes in *a* reflected changes in the animals' motivation to perform the responses at a higher force requirement. This could possibly be due to rewarding or aversive properties of the operant response relating to the different force requirements. In Killeen (1975) neither deprivation levels nor the quality of the reinforcer was manipulated across conditions which would mean, theoretically, specific activation and the rate of reinforcement should remain constant. However, response rates fell well below their theoretical asymptote (where they cease responding in this case) and varied substantially due to the contingencies that either reinforced or punished the target response. In Bizo

and Killeen (1997) it was clear longer reinforcer durations (2.5-s vs 5-s) engendered more responding and effected *a.* The specific activation parameter increased with longer access to food. However, doubling the incentive value may require more than doubling the amount of reinforcement. This is consistent *with the paradoxical incentive effect* which identifies that organisms don't always necessary respond faster for more food (Bizo et al., 2001).

The reasons for these unusual findings are unclear. Such findings have led investigators to suggest that increasing the force required to obtain a reinforcer is similar to adding an aversive consequence to the response (Alan & Poling, 1995; Bjarnesen, 2011)**.** Bjarnesen (2011) suggested that it was the change in operandum, rather than the change in force requirement that prompted the change in motivational state. There is support for the theory that the hens received some form of automatic reinforcement or punishment from performing the target responses. It is reasonable to assume (but it is not a definitive conclusion) that increasing the physical effort required to emit a response increases the aversiveness of responding. Consistent with this notion, some investigators have suggested that the effects of increasing the force required on an operandum are comparable, in at least some regard, to those of punishment (Alling & Poling, 1995; Chung 1965). Punishment is a decrease in the future probability of a specific response as a result of the immediate delivery of a stimulus for that response (in this case delivery of a high force requirement). Although, given this kind of definition, increasing response force cannot literally constitute punishment, it may however, have similar response reducing behavioural effects. This may also explain why at the higher force requirements the break point is generally at much lower FR's. The animals may cease responding earlier due to the punishing

properties of the response itself. This is also evident in Bjarnesen (2011) in that response rates were similar when the force requirement was increased despite operandum. Additionally, in the present experiment, the high force requirement may have been more aversive and therefore outweighed the gain from the increase in reinforcer duration. Regardless of operandum in Bjarnesen (2011) and duration of reinforcer in the present experiment the high force requirement was a common factor that produced lower response rates and break points.

Specific activation is attenuated by the inverse square law; variations in the motivation levels when motivation is low will have a greater effect than variations in the motivation level when motivation is high (Killeen & Sitomer, 2003). This means that changes in the *a* parameter will be greatest when motivation is small and less significant when motivation is higher. Changes in *a* are also proportional to ratio size with bigger effects being evident at bigger ratios. In the current study the estimated *a* values corresponded to the highest ratio achieved by each individual hen. All the hens in the present study responded to FR512 in the low force, small reinforcer condition. In the other conditions; high force, small reinforcer and high force, large reinforcer the FR values that the hens' ceased responding at varied considerably (between FR32-512). This may account for the significance of the *a* parameter. This also shows that the hens had low motivation in general, therefore showing a significant effect of the *a* parameter.

Taking into consideration the evidence, force requirement may be a component implicit in the *a* parameter rather than the δ parameter. The aversive properties of the increase in effort required may impact on the motivation to respond therefore impacting on specific activation rather than constraint. This research along with the only two studies looking at specifically manipulating

force requirement and modelling the effects with MPR (Bjarnesen, 2011; Bizo & Killeen, 1997) came to the same conclusions; the increase in force decreased arousal. Therefore, it can be concluded that force requirement (effort) did not affect the constraint parameter to a significant level as expected but rather effected specific activation- which equates to a decrease in arousal and motivation. Covarrubias and Aparico (2008) accurately predicted performance with rats responding under PR schedules and also found unanticipated findings where the *a* parameter was higher for the higher PR. It was suggested that the *a* parameter may be effected indirectly by motor parameters of the task. Because of the suggestion of differentiation of the two roles of response duration (time and effort) Bizo and Killeen (1997) thought it important to replicate their findings with different techniques; using a VR schedule. They showed that most of the differences in δ were accounted for by changes in the response duration not the increase of force**.** The value of *a* did not remain invariant with response topography which can be explained by MPR only if response effort is not proportional to response duration.

There have been suggestions for alternative models of *a* by Killeen, himself and Bittar, Bittar and Del-Claro (2012). MPR predicts that when *a* increases the slope of the curve should not change (See Figure 1). However, in Bizo and Killeen (1997), the slope of the curve 1/*a* decreased (flattened) threefold, with *a* going from 64 for key pecking to 196 for treadle pressing. This compensates for the threefold increase in delta, so that the x intercepts of the two conditions are comparable. This is inconsistent with the theory, which predicts that the unnormalised curves will be congruent and thus normalised. By scaling up the ordinate for treadle pressing that curve should show a much faster decrease

(Bizo & Killeen, 1997). Why the failure of the prediction? One of the basic assumptions of MPR; its first principle, is that the strength of responding is directly proportional to the duration of the target response. This assumption is built into the equation. If the first principle had posited the dependence on reinforcement rate alone, then the slope of the curve would have predicted to be not 1/a but rather 1/( δ *a). This latter curve is just what was found in Bizo & Killeen (1997). As the treadle involved a larger response time, if you divide the seconds of responding that the reinforcer would elicit and divide it by the actual time it took to make a response, then the number transforms. Killeen (1994, Footnote three) states that response duration does not always capture the energetic requirements of a response, which is of concern for the first principle. Alternatively it may take a minimal amount of activation (k) to initiate a response, which would entail a relation such as:

$$B = \frac{a*r}{k+\delta} \quad (4)$$

Another alternative model for arousal has been proposed by Bittar et al., (2012). The assumptions used to derive their formal model of arousal dynamics were as follows (a) reinforcers arouse organisms, (b) the arousal decays over time, (c) the arousal accumulates, (d) reinforcers lose their arousal effect through successive presentations and (e) there is a limit to the degree an organism can be aroused. The assumptions also included (f) a fraction of *C.* of an organism's arousal is directed to emission of target responses and (g) time constrains responding; two principles at the heart of MPR. Although the majority of these are

at the core of MPR they exclaimed that the process by which successive reinforcer presentations affect arousal are not clearly devised leading MPR to a modelling mistake.

While Bittar et al., (2012) maintained the assumption that organisms behave under constraints; they proposed to consider arousal itself to also be constrained. They demonstrated that by representing arousal as a parameter in the range of 0-1 then they could formalise MPR in the simplest and most intuitive form. In MPR arousal is directed by coupling to produce operant responding (Killeen, 1994; Killeen & Bizo, 1998) while operant responding in turn is constrained by time. This point is important; time constrains responding, not arousal. MPR takes arousal as a linear function of reinforcement (that is it is proportional to operant responding). To limit the increase of arousal, Bittar et al., (2012) considers it as a variable that ranges from 1-0. The reasoning behind this proposal is that the hypothesis that organisms can be unlimitedly excited seems unreasonable from a biological view point (satiation emphasised). The arousal value is multiplied by its distance to the ceiling. In this way when arousal is low its growth is not significantly restrained because the ceiling is close to 1. As arousal rises the distance to the ceiling decreases and growth is heavily restrained. This models a process where reinforcers add arousal and satiation subtracts the arousal adding effect of the reinforcers, up to a point, where it begins to dissipate according to its natural cause. More over arousal is presented here as a dimensionless variable with range 0 (no arousal at all) and 1 (maximum arousal supported by the organisms biology). Equation 5 is the simplest possible formalisation of Killeen's theory of operant behaviour proposed by Bittar et al., (2012) incorporating his three principles arousal, constraint and coupling. The

relations are immediately clear: the response rates (B) are directly proportional to the time it takes to make a response.

$$B = \frac{AC}{\delta} \tag{5}$$

The product of A and C represents the amount of arousal directed to emission of target responses. For example; a hypothetical situation where the animal is totally aroused (A=1) and where there is perfect coupling (C=1) we would expect to obtain the maximum response rate obtainable. This maximum response rate can be represented 1/δ, where δ is the time required for the emission of a single response. Therefore, six assumptions were formally elaborated in their model (1) the arousal impulse (2) the time constant of arousal decay (3) the constant of satiation, (4) the coupling coefficient (5) the response duration and (6) the rate of reinforcement.

Application of this model to experimental data from different laboratories demonstrated generality. Comparison with other models attested to its adequacy. The model provided a good description of the responding of rats and pigeons working for different reinforcers under different experimental conditions, although focused predominantly on VI schedules and within session responding. The parameters of the equation changed in the predicted ways when they were fitted to the behavioural data. The arousal impulse correlated with the reinforcers magnitude. The constant of satiation correlated with the reinforcer magnitude, with the organism's capacity and sometimes the rate of reinforcement and the response duration correlated with the force required to make a response. So while

Killeen proposes a minimal amount of activation to initiate a response, Bittar et al. (2012) proposes a ceiling on specific activation in regards to within session changes in arousal.

Lambda; λ tells us the average number of responses that are coupled to a reinforcer in memory, which translates to short term memory. It was predicted that λ would increase with the increase in force requirement as this was expected to impact on the δ parameter; the duration of the response was expected to be longer and therefore takes up more memory. The parameter λ positively covaries with the duration of the response it weights (Killeen 1994; Bizo and Killeen, 1997). These two factors would mean that there would be less association between the response and the reinforcer with longer periods of non-responding and other behaviours occuring; decreasing the coupling-coefficient. The estimated values of λ in the present study varied depending on the hen. Overall the average estimates of λ increased with each condition, as would be expected. For 4 of the five hens λ was highest in the high force, large reinforcer condition. Lower response rates were also associated with the larger reinforcer magnitude at the small FR's, generating smaller estimates of λ. Reilly (2003) also found that estimates of λ changed with an increase in the quantity of the reinforcer.

Taking a further look at Bizo and Killeen (1997) and Bjarnesen (2011) it is evident that there were positive correlations between the λ and δ parameters consistent again with the present data, although this is not explicitly reported. Memory of the target response is assumed to be displaced during the consumption of a reinforcer explaining why λ would increase with larger reinforcers. Bizo et al., (2001) also demonstrated that the size of the pellets affected the λ parameter, with smaller reinforcers resulting in higher response rates and higher λ estimates**.** An

explanation for this includes consideration of the consummatory behaviour, particularly in regards to quantity, where larger pellets or longer access occupy more memory. Manipulating the duration of an incentive should affect more than the activation levels (Killeen & Sitomer, 2003). Brief incentives do not completely reset the response memory. As the incentives duration is extended it should increase *a* as well as effectively erase memory for the prior target response, thus having mixed effects. Increased magnitude does effect *a*, however, it also increases erasure of prior response traces. Additionally, although consummatory and post consummatory behaviours are not target responses they displace the memory for earlier responses. The delivery of reinforcement decreases the ability to subsequently discriminate whether the target responses caused the delivery of the reinforcer. Killeen and Smith (1984) showed that this overshadowing increased with the duration of the reinforcer up to durations of 4-s, where discrimination actually approached chance.

There are a number of limitations with this research. Some of the irregularities in the matches shown in this paper and one of the major limitations were due to the sample size that constituted the database. Because there were only five hens in each condition the data is noisy and lacks statistical power. Another limitation includes increasing the force requirement having two effects: there was an increase both in the force required for reinforcement and in the force required for a response to be recorded. It may have taken some hens more pecks to make the response, therefore as force requirement varied the response definition implicitly changed. To the extent of response force is of an interest as an independent variable, the conflation of response force and response definition is unavoidable. It is however possible with the appropriate equipment to record the

actual force of each response, and to present data showing how force distributions change as a function of changes in required response effort.

Covarrubias and Aparico (2008) found that *a* was significantly affected by step size but not reinforcer quality. Geometric ascending step sizes resulted in large increases in FR value from one day to the next. It would be interesting to see how the different step sizes effect responding as well as PR schedules within sessions. Only one day per FR value would have allowed another series on the different force requirements. Reilly (2003) describes progressive ratio schedules as more efficient because a complete ratio function can be generated in a single session; however, they tend to produce systematic deviations from MPR , which is not quite understood why.

Because schedules of reinforcement are generally held constant throughout the session, observed variations in response rate must be primarily attributed to changes in processes such as arousal, satiation and habituation. As a consequence, within session data provide a valuable means to clarify the relation between performance and important motivational variables. This may be useful to isolate the effects of force requirement and its contributing factors to motivating operations and arousal. Because multiple session exposure at each FR value did not greatly affect response rates it would make sense to only expose the organisms to one day on each. The benefits of multiple exposures to each FR values do not justify the cost, particularly in terms of time. It would be interesting to investigate the interactions between different step sizes, force requirements and durations of reinforcers.

MPR is a theory of reinforcement schedules and allows description and prediction of behaviour. It consists of three key parameters, each identifying a

different causal factor in the control of behaviour. The parameter *a* tells us the number of responses that can be activated or elicited by each incentive and thus provides a measure of arousal and incentive motivation. The parameter δ tells us the number of seconds it takes to make a response and thus constitutes both the lower limit of an IRT and the reciprocal of the maximum attainable response rate. The reciprocal of λ tells us the average number of responses that are coupled to a reinforcer in memory. This experiment aimed to increase the force requirement and the duration of the reinforcer which was predicted to increase the δ and *a parameters*, respectively. Five hens responded on a geometric FR sequences in three conditions; low force, small reinforcer, high force, small reinforcer and high force, large reinforcer. There was the expected bitonic pattern of response rates as predicted on FR schedules. Hens' response rates and break points decreased with the increase in force requirement. There was no consistent effect with the increase in reinforcer duration. The δ parameter did not significantly change with an increase in force requirement as expected, however, there was a significant increase in *a.* Estimates of *a* did not change when the quantity of the reinforcer was increased as one might have expected given the results of previous experiments. Results are consistent with the only two studies (Bizo & Killeen, 1997; Bjarnesen, 2011) specifically manipulating force and predicting response rates with MPR. There are mixed findings on the effect of magnitude on reinforcer effectiveness. It may be due to displacement in memory of the target response. Due to these results it is proposed that force requirement is a variable that effects motivation and arousal rather than constraints on responding. Although there was a major limitation in regards to the sample size in the present research which makes it difficult to make definitive conclusions. Recommended

future research would consist of isolating force requirement in relation to arousal and constraint.

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**Appendix A**

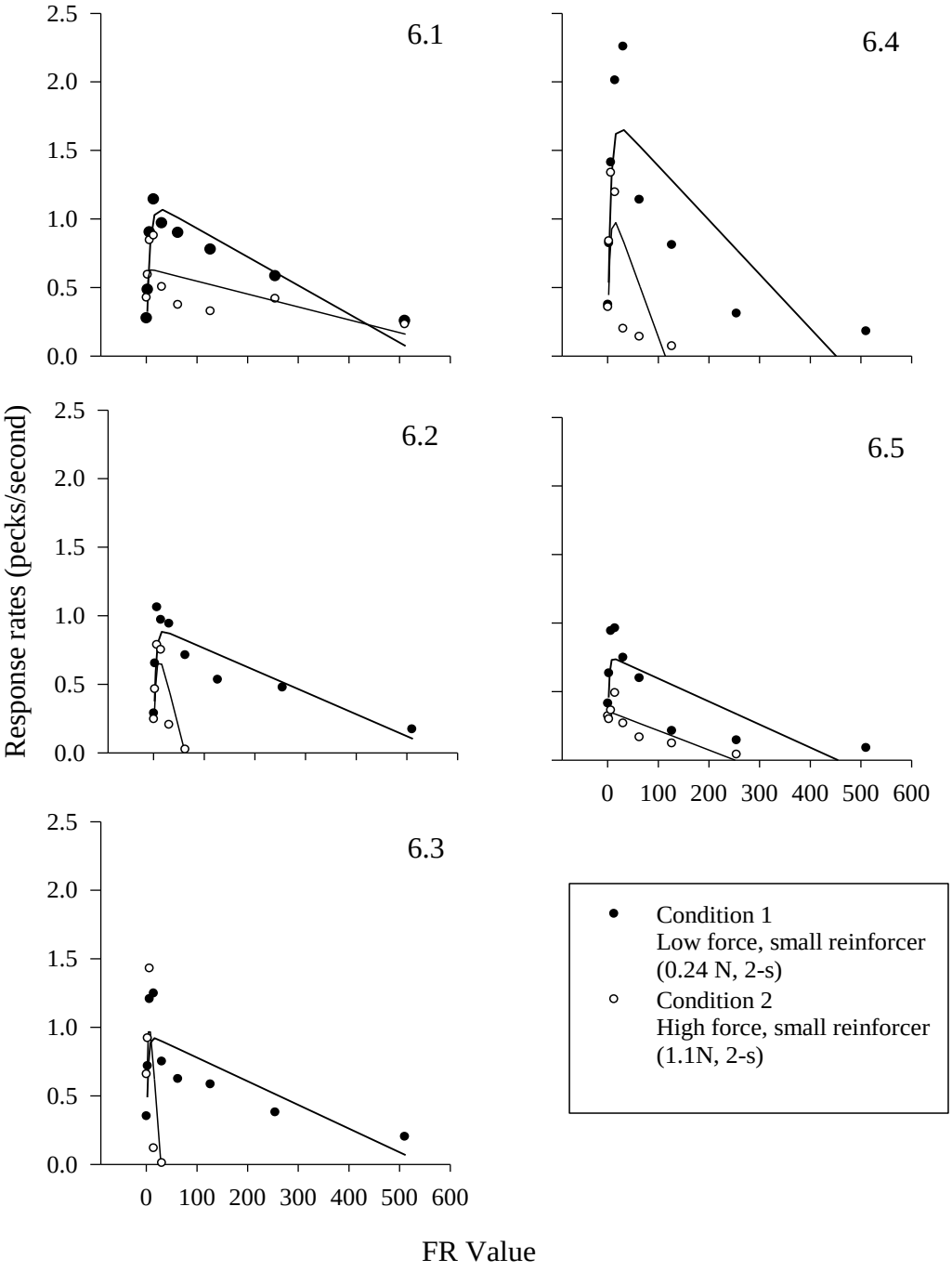


*Figure 6.* Each individual hen's response rates are plotted as a function of FR values. These values are calculated by adding the total number of key pecks and dividing this by the total key time for the last three sessions. The lines show the values predicted by equation 3. The filled circles show actual response rates for Condition 1; low force requirement, small reinforcer duration (0.24 N: 2-s) and the unfilled circles represent the actual response rates for Condition 2; High force requirement, small reinforcer duration (1.1 N: 2-s). Graph does not start at 0 for clearer representation of response rates at the lower FR values.

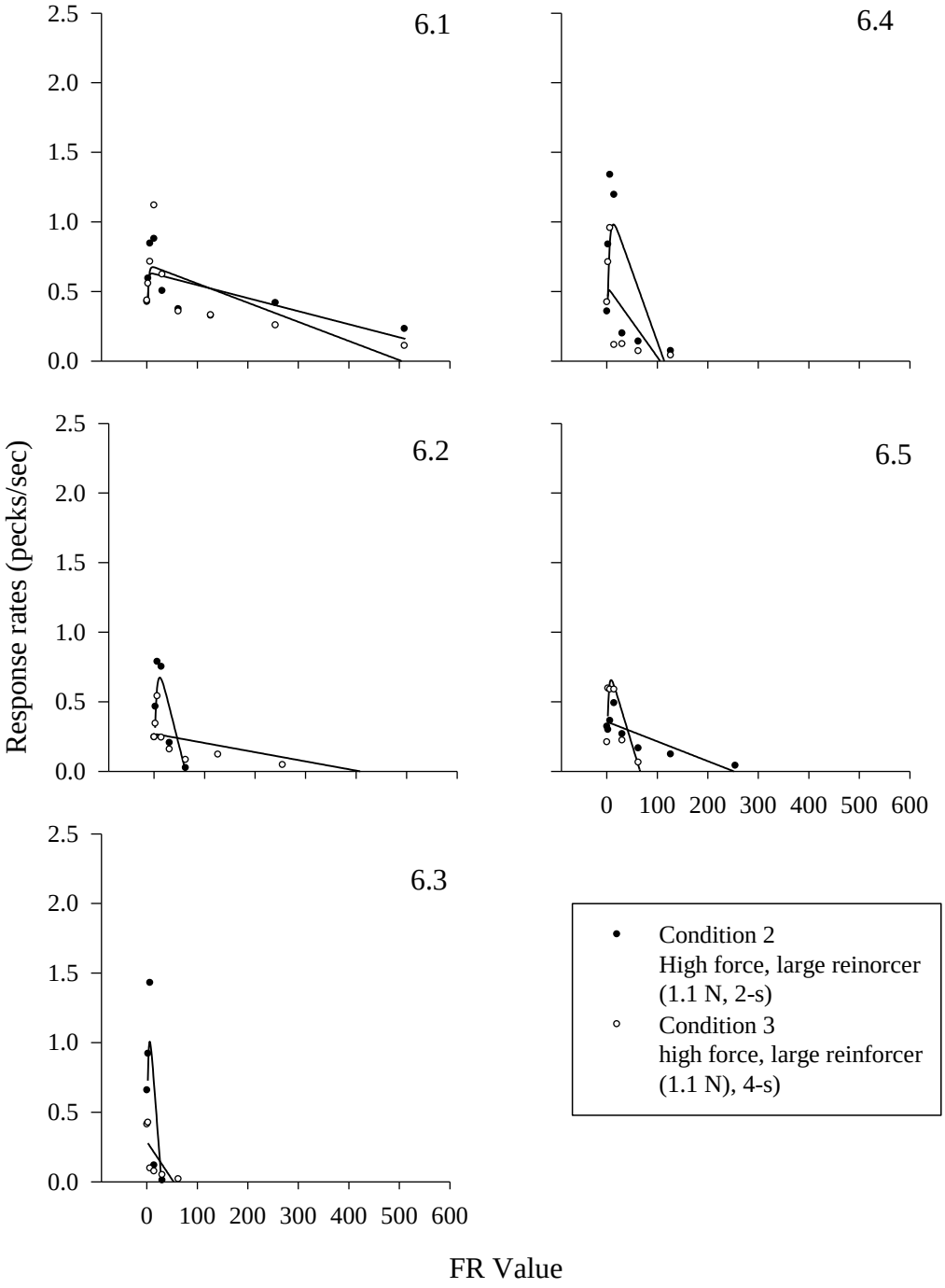


*Figure 7.* Each individual hen's response rates are plotted as a function of FR values. These values are calculated by adding the total number of key pecks and dividing this by the total key time for the last three sessions. The lines show the values predicted by equation 3. The filled circles show actual response rates for Condition 2; low force requirement, small reinforcer duration (1.1 N: 2-s) and the unfilled circles represent the actual response rates for Condition 3; High force requirement, small reinforcer duration (1.1 N: 4-s). Graph does not start at 0 for clearer representation of response rates at the lower FR values.

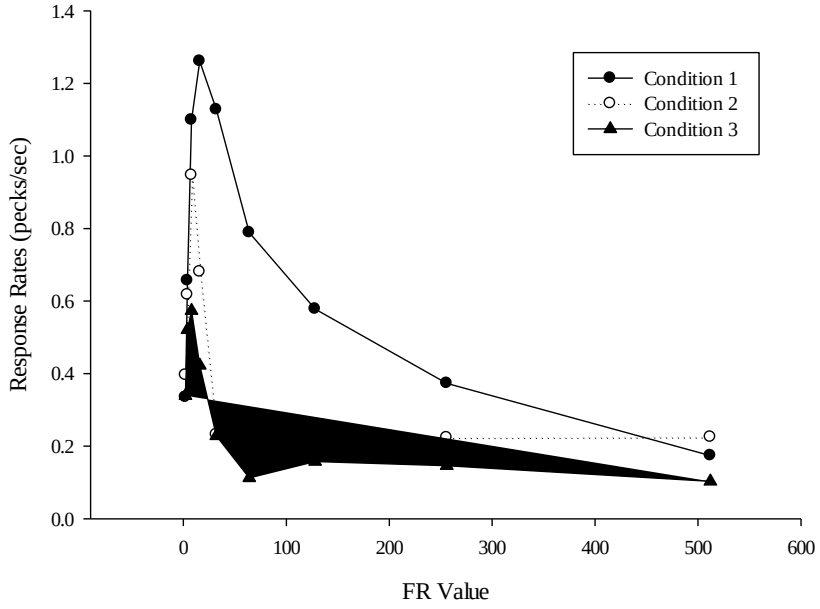


*Figure 8.* Average response rates across FR values for all hens in all conditions.

## Appendix B

Pilot study with alternate key design

The chamber was the same as the one used in Experiment one and two. The alternative response key was located 50-mm to the right of the food magazine at a 45 degree angle from the floor of the chamber (see Figure 9). This key was designed to simulate more naturalistic responding. The subjects were the same as the ones used in Experiment one and two with the exception of an extra hen that died and was not replaced. The FR values used were a Fibonnacci series, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144 and 233. Each hen was on the FR value for at least five days. The average response rates of the last three days was used as the measure in this study, this data compared to the first three days were similar. The force requirement was 0.20 and was measured on a weekly basis to ensure it was consistent. The procedure of running was the same as in experiment 2.

After a period of data collection it became apparent that response rates were highly variable (See Figure 10 and 11). This was due to the topography of responding on this key. This was confirmed through direct observation of the hens responding and the response key was subsequently changed. Rather than pecking the key, behaviours consisted of more scratching at the key which did not register as a response. It was not that the animals were less aroused but rather our monitors were not differentially sensitive to certain response topographies. Additionally, scratching behaviour did not allow for the key to go back to resting position.

Killeen (1994) highlights that effective conditioning requires a correlation between the experimenters definition of a response and an organism's but the animals perceptions of its behaviour differ from ours. Reinforcers effects are not

only limited to the response that immediately preceeded it. The scratching behaviour intermittently resulted in registering as a response and therefore there seemed to be a discrepancy between our definition of a response and the behaviour of the hens. Because reinforcement acts on everything that the organism does that is contained in its memory, which may not be the target response defined by the experimenter, it means that the other behaviour the animal performed was also reinforced. Because we take vigor of the activity as an index of arousal this key did not prove to be an adequate measurement and was not representative of the animal's behaviour.

As can be seen in Figure 10 and 11 response rates are varied, increasing and decreasing over FR values. This is inconsistent with the bitonic pattern of responding typical of hens responding on FR schedules.

*Figure 9*. Photos showing the Floor key in the experimental chamber with a chicken present for perspective.

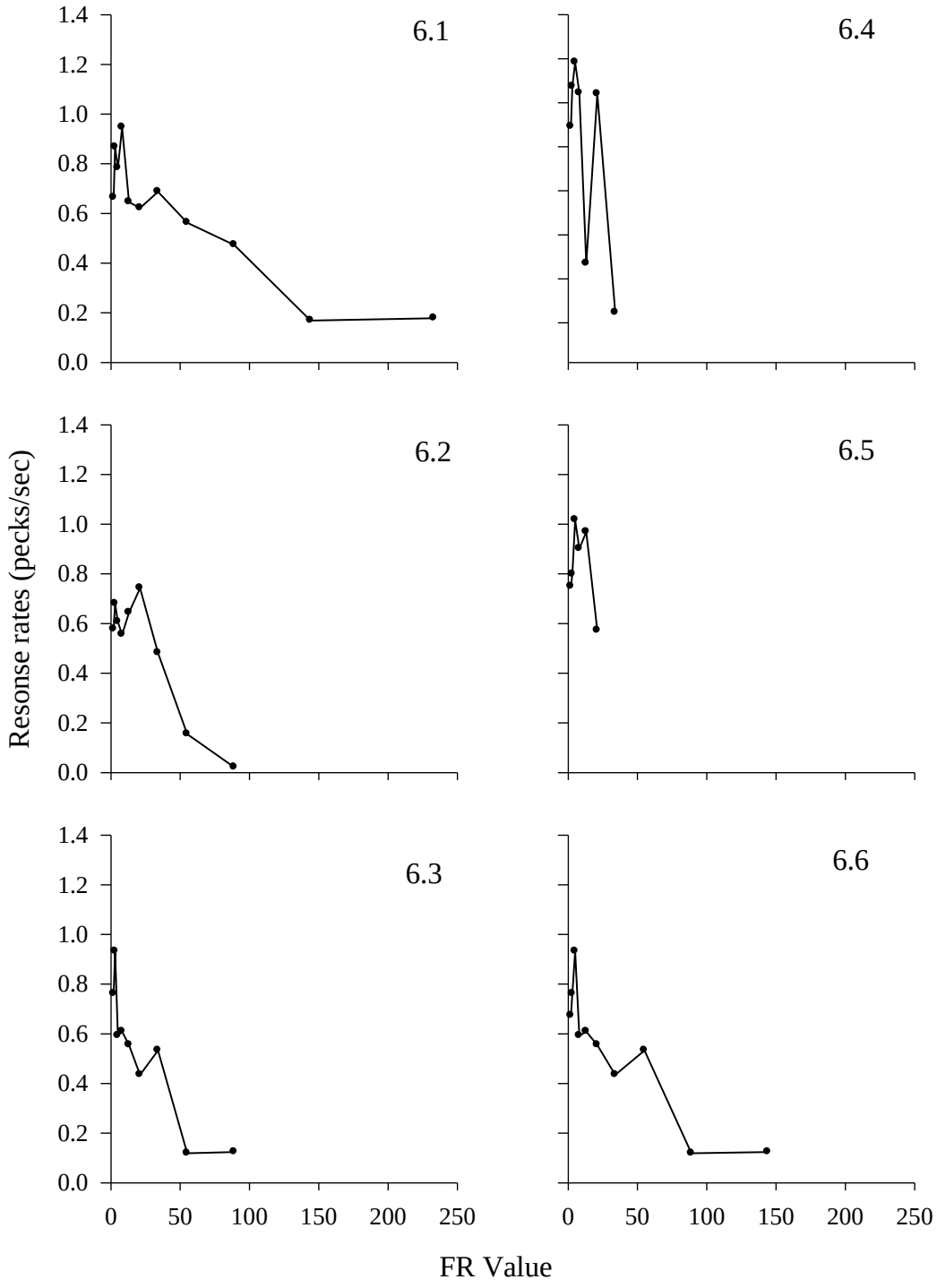


*Figure 10.* Each individual hen's response rates are plotted as a function of FR values for responding on the floor key. These values are calculated by adding the total number of key pecks and dividing this by the total key time for the last three sessions.

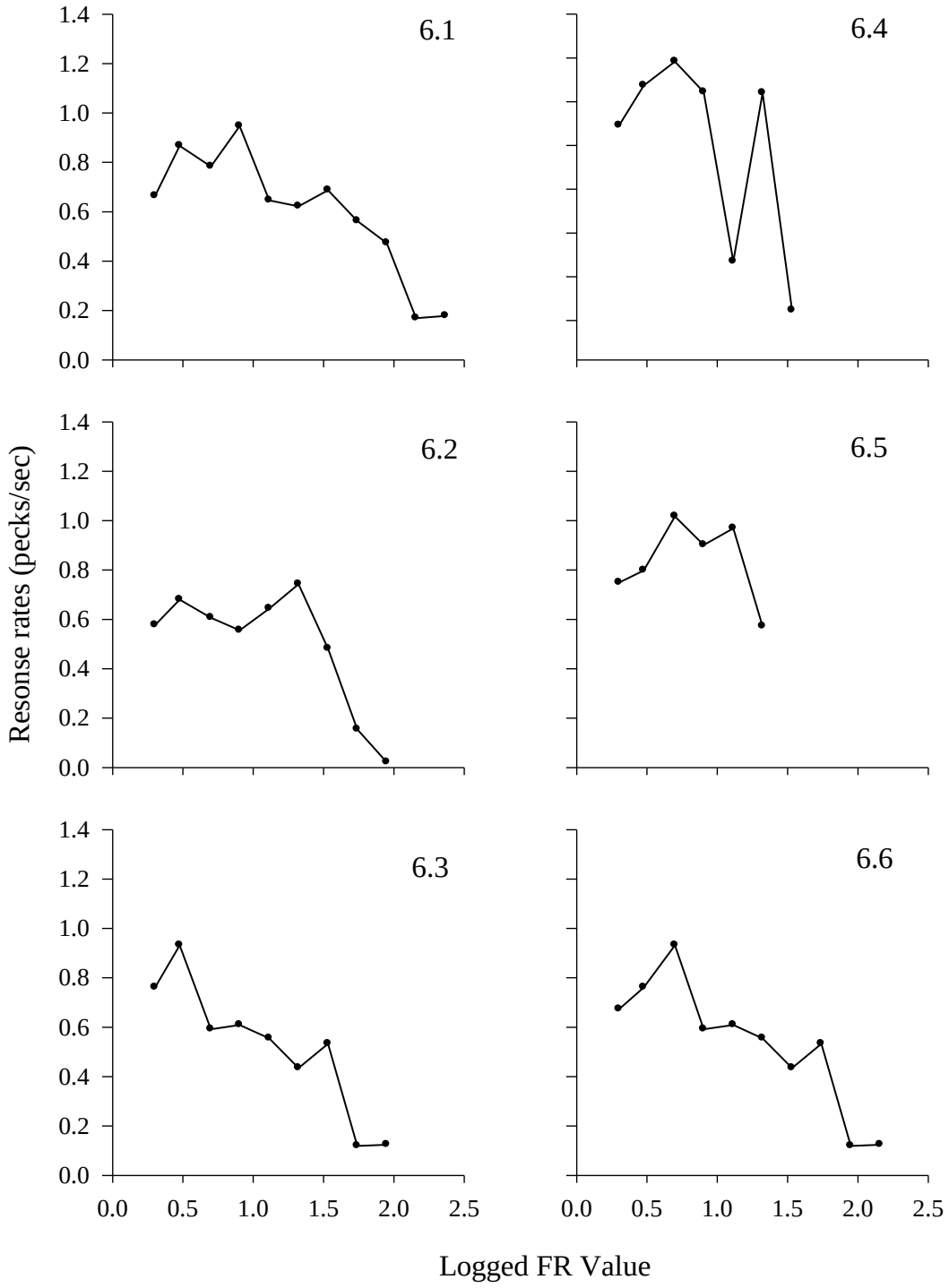


*Figure 11*. Each individual hen's response rates are plotted as a function of logged FR values for responding on the floor key. These values are calculated by adding the total number of key pecks and dividing this by the total key time for the last three sessions.